Bk. 5

W. RALL

5

RECORD

7530-222-3525
FEDERAL SUPPLY SERVICE
(GPO)

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9/18/64

Book 5

Continuation of Research Diary.

Book 4 ran from 3/11/64 — 9/17/64

Summary of Contents

9/21/64

Summarize and review the computations that were set up 9/17/64 and run on 9/18/64, which are getting close to optimal runs suitable for publication.

64794.8837&8 compare with 35&36 p. 90 of Book 4
33&34 p. 84 of Book 4
This is an attempt at decremented dendritic spike.

.8837 The inhibition was too strong for cpts 7-14
note also that axonal spike overshoots too strongly.
This means that ROUTC should go back up to 10.
and ~~will~~ make the present amount of C less effective.
∴ for 39 Try ROUTC=10. and ~~C=0.5 for cpts 7-14~~
also reduce AFPOS to .08 NEJ=1 for cpts 4-14
C=.4, .5, .6 . . . . 1.4

.8838 differed from 37 only in having I.C. = 0.1 in dendrites.
This made them fire earlier, but not bigger spikes.
next time, try .05 for this

New Series to be 8851 & 52. CRT for a production run

64794.8841 ~~NJD=5~~ Active ~~Descending~~ I.C. Blocked
53 " " double I.C.
54 toted same with USA=5, USD=200, NSTEP=10
55 old 43 with NJD=10, but + doubled I.C.

64794.8842 NJD=5, Passive Ascending I.C.
44 10
56-59 ROUTB=50 need more ROUTB & French
DT=.02 I.C. & USA=5, USD=200.

9/21/64

Series 64794.8741, 2, 3 & 4 cooler kinetics

.8741 NJD=5 ~~Active~~ I.C. .2, .16, .12, .08, .04, 0
got some delay & then almost synchronous spike
increase Cdy 20%
* also got reflected orthodromic

.8742 (5) passive I.C. .2, .3, .4, .4, .4, .3
main spike story pretty good but
got a second spike.
need more quench or ROUTB
make ROUTB = 40.

.8743 NJD=10 Active
Pretty good (slight reflection in (3))

.8744 (10) Passive pretty good but needs
more quench

Setup as 45, 46, 47, 48

in each, increase ROUTB to 40.
NSTEP to 15
USA = 5.
USD = 200.
NPLT = 3 LJZPLT = 3
IFTEST = 10311

for NJD=10 get 112

for ~~NJD~~ NJD=5

estimate that computation of (NT=41)(NSTEP=20) = 90 sec
table 5 sec
~~3 plots~~ 95

for NJD=5 NZ=9

get 120 for NJD=10 NZ=14

Three plots take 18 ~~minutes~~ secs

IFTEST=10311 should cost ≈ 50 secs
45 for NJD=5
65 for NJD=10

∴ estimate a ~~total~~ of about 160 secs for a run with NJD=5
205 secs =10

for NT=41, NSTEP=20, NPLT=3.

However for NSTEP=10, would have the 90 for NJD=5 & save 45
112 55

9/21/64 Time Estimates 4

early guide estimates

Set up 64794.8851 #2 as CRT (decremental cond.)

Set up following as a Production Run

	NT	NSTEP (NSD)	NPLT	IFTEST 103111 in most cases	Time	Pages
64794.8853	41	20 (5)	3	220	160	10
DT=.01 54	41	10 (5)	3	150	120	10
55	41	10 (10)	3	150	150	10
DT=.02 56	41	20 (5)	3	220	160	10
57	41	20 (5)	3	220	160	10
58	41	20 (10)	3	220	210	10
59	41	20 (10)	3	220	210	10
.8745	41	15	3	180	140	10
46	41	15	3	180	140	10
47	41	15	3	180	180	10
48	41	15	3	180	180	10
				2120	1810	110 pages
				37 min	30 Min	

CORE

742 Write Output Tape, 15, 743
743 Format (H CONE RESISTANCE EFFECT IS SKIPPED HERE. ( )

~~744 IFCONE=0 GO TO 899~~

747 IF (IFPLVE) 640, 645, 645
640 CONE = 0
641 GO TO 696
645 CONE = 1   646 GO TO 653

9/21/64

Plan to Modify WXR794C → WXR795C

By revising extracell calc & incorporating it in Subroutine WXR95C.

Four stages
① (1000) without external shunt
② (1100) with potential divider but ∈ shunt zero
③ (1110) with significant shunt current
④ (1111) radial Re of cone

see p. 12

IFVE = 1111 means compute and tabulate all stages
2222 means also plot all stages.
1112 ~~means~~ plot only last stage.
1002 means do not tabulate 2nd & 3rd stage.

WXR95C (NT, NZ, KG, NG, JS, JH, ~~CORE~~ NJD, NKZ
(KVE, IFVE, IFPLVE, IFAB, VEF, CORE,
Dimension (PDF, SHCF, RHOSOM, RHOGLM

101 GO TO (704, 740, 800, 850, 899), KVE
704–722 same as in 794C except replace 2.5 by VEF
725 becomes new number of 726
727 becomes IFPLVE = IFVE/1000
~~728 IF(IFPLVE) 729, 729, 730~~
~~729 IFPLVE = 1~~
738 RETURN

740 IFVE = IFVE − 1000*IFPLVE
741 IF(IFVE) ~~742, 811~~, 745
746 IFPLVE = IFVE/100
~~743 IF(IFPLVE) 744, 744, 745~~
~~744 IFPLVE = 1~~

~~800~~
~~811, 853, 853~~
~~745 GO TO 853~~

In main prog.

Old 560 to become 561

replace 5601 with 560

in 536 replace 560 by 551

~~replace 530 ahead of 530 above~~

~~525 IF~~

670 IF(IFPLVE) 531, ~~660~~ 659, 531

555 IF(IFPLVE-1) 659, 659, 560

659 CALL NIH104 (ICLOCK, JCLOCK)

~~661~~ Write Output Tape 15, 999, JCLOCK

660 as before

661 IF (KVE) 662, 662, 666

662 IF (VEF) 663, 663, 664

663 VEF = ~~2.5~~ 3.0

664 VMIN = -VEF

665 VMAX = 1.2 * VEF

666 KVE = KVE + 1

667 old 662 666 not numbered

668 CALL WXR95C (arg

~~670 IF (KVE) (4-KVE) 800, 670, 670~~

668 IF (4-KVE) 800, 668, 668

9/21/64

```
745  IF (PDF) 746, 746, 747
746  PDF = 0.25
747  F = PDF / (PDF + 1.)
750  like old 750 with PDF added
751  modified + with F10.5 added
     omit VMAX & VMIN
752 - 780 as before except { JS in place of 1
                           { -F " " " -.2

781  RETURN
```

```
800  IFVE = IFVE - 100 * IFPLVE
801  IF(IFVE) 899, 899, 802
802  IFPLVE = IFVE / 10
803  GOTO 745
804  IFPLVE = 1
805  IF (SHCF) 806, 806, 807
806  SHCF = 0.2
807  F = SHCF / (SHCF + 1.)
809  DO 880 KT = 1, NT
810  PA = F * (VATZ(KT, JS) - VATZ(KT, NZ))
861  DA = PA
862  JZ = NZ
865  DO 870 I = 1, NZ
866  VATZ(KT, JZ) = VATZ(KT, JZ) - CA
867  CA = CA + DA
868  JZ = JZ - 1
870  IF(AB) 820, 820, 820
820  same set for B
880  CONTINUE
```

808 XD = 1/NJD

IF(IFAB) 810, 810, 812

812 CA = DA

867 fast for CONE AC(JZ) = DA * BC(JZ)

see over

881 Write Outpt Tape 15, 882, SHCF

882 Format(H Following VE Correspond to an External Shmd Factor of, F10.5)

883 RETURN

$= \frac{XNJD\,(RHOGM * RHOSOM)}{RHOGM - RHOSOM}$

$F = \frac{XNJD}{\frac{1}{RHOSOM} - \frac{1}{RHOGM}}$

668 $X^{JD} =$ ~~1/NJD~~ NJD

669 $X^{JD} = X^{JD} * XD$

~~670 F = RHO * XJD~~ $F = (RHOSOM * RHOGM) / XJD$

671 DO 672 JZ = 1, NLZ

672 BC(JZ) = F * (AB(JZ) - AB(JZ+1))

673 IF(AB) 674, 674, 683

674 DO 683 KT = 1, NT

~~675 DO JZ = 1, NLZ~~

675 JZ = NLZ

676 DO 678 I = 1, NLZ

677 AC(JZ) = BC(JZ) * (VATZ(KT, JZ) - VATZ(KT, JZ+1))

678 JZ = JZ - 1

679 JZ = NLZ

680 DO 682 I = 1, NLZ

681 VATZ(KT, JZ) = AC(JZ) + VATZ(KT, JZ+1)

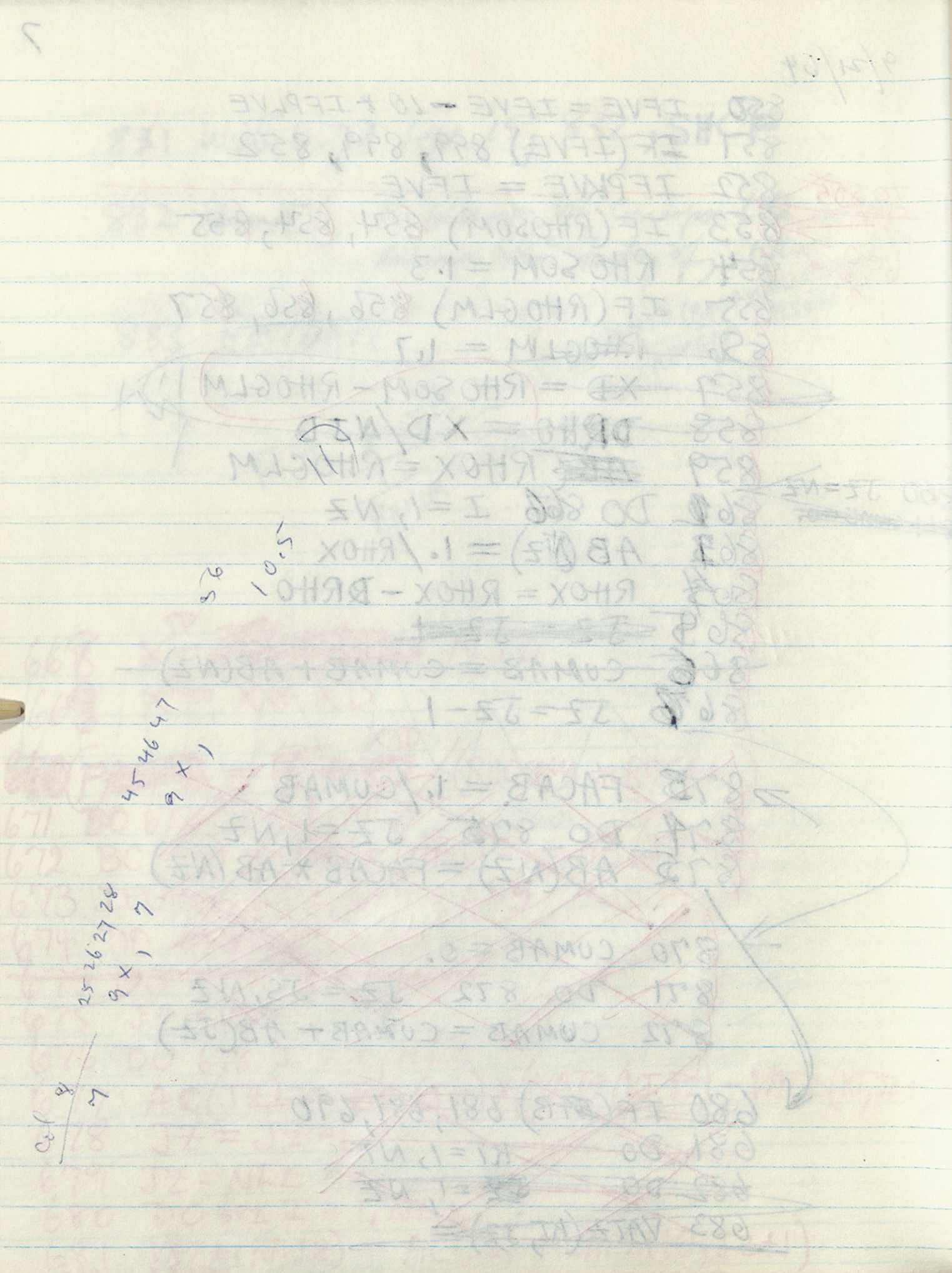
682 JZ = JZ+1

9/21/64

```
      IFVE = IFVE - 10 * IFPLVE
      IF (IFVE) 899, 899, 852
      IFPLVE = IFVE
      IF (RHOSOM) 854, 854, 855
      RHOSOM = 1.3
      IF (RHOGLM) 856, 856, 857
      RHOGLM = 1.7
      XD = RHOSOM - RHOGLM
      DRHO = XD/NJD
      RHOX = RHOGLM
      DO 866 I = 1, NZ
      AB (NZ) = 1./RHOX
      RHOX = RHOX - DRHO
      JZ = JZ - 1
      CUMAB = CUMAB + AB(NZ)
      JZ = JZ - 1

      FACAB = 1./CUMAB
      DO 875 JZ = 1, NZ
      AB(NZ) = FACAB * AB(NZ)

      CUMAB = 0.
      DO 872 JZ = JS, NZ
      CUMAB = CUMAB + AB(JZ)

      IF (IAB) 681, 681, 690
      DO KI = 1, NT
      DO JZ = 1, NZ
      VATZ (KI, JZ) =
```

GO TO 855 otherwise by 600 series

860 JZ = NZ
861 CUMAB = 0.



9/21/64 ~~683 CONTINUE~~

~~682 JZ = NZ~~
~~683 DO I = 1, NZ~~
~~684 AC(JZ+1) = AB~~
~~684~~

683 IF(IFAB) , 684, 684
684 similar for BB

694 Write Output Tape 15, 695, RHOSOM, RHOGLM
695 Format (CH following VE include Conical Resistances for RHOSOM=, F10.5, CH AND for RHOGLM=, F10.5 /) and F=

696 RETURN

863

870 DO 871 , JZ = 1, NZ
871 AC(JZ) = DA * BC(JZ)
872 CA = ~~AC(NZ)~~ DA
873 JZ = NZ
874 DO 877 I = 1, NZ
875 VATZ(KT, JZ) = VATZ(KT, JZ) - CA
876 CA = CA + AC(JZ-1)
877 JZ = JZ - 1
~~879~~ 879 IF(IFAB) 898, 880, 880

9/22/64 These cards punched today.
Now complete

Col7

SUBROUTINE WXR95C (NT, NZ, KG, NG, JH, JH, NJD, NLZ
X KVE, IFVE, IFPLVE, IFAB, ~~IFFE~~ CORE,
X VEF, PDF, SHCF, RHOSOM, RHOGLM
X VATZ, VBTZ, AB, AC, BB, BC,

Dimension VATZ(251, 14), VBTZ(251, 14),
AB(14), AC(14), BB(14), BC(14)

Also for extra input card
2442 write output Tape 15, 904

2441 IF(IFVE) 245, 245, 2442
2443 Write Output Tape 15, 936
936 Format (9X, 3HVEF, 7X, 3HPDF, 6X, 4H
↳ SHCF, 6X, 6HRHOSOM, 4X, 6HRHOGLM, /)
6X, 4HCORE
2444 Read Input Tape 1, 956
x 956, NC, VEF, PDF, SHCF, RHOSOM, RHOGLM,
CORE
956 Format (I1, 4X, 6F10.5)
2445 Write Output Tape 15,
x 956

This will permit different soma threshold

replace CORE on card 3 with RSOK

Set RASO = RACT * RSOK

Open Shop Production Runs
Control # 91000

9/22/64

~~Hot kinetics with active case gave too much much of(?) pos, otherwise good.~~

64794.8854 was pretty good active with hot K.
dendritic spike nearly synch.
slight electronic reflection

might increase some I.C to .3
eg. .3, .25, .20, .10 .0 .0

64794.8855 got too much pos. aft. * 0.5 in aft. 1

* got neg E (i.e. neg B) in main prog from active R.K. sub.
also got this was Passive RK

Also cooler kinetics do this

fix subroutines to prevent B going neg.

~~See previous page~~

in 93C & 94C

```
465  IF (B(JZ)) 4651, 4661, 4661
4651 DB = - B(JZ) /DELT
4652 GO TO 467
```

This should eliminate neg B

Probably can manipulate heat with RBFR
threshold with RBSQ
for any given value of RACT

See also p. 58 of Book 4 & cf. p. 35 of Book 24

	Hot	Cool
RACT	600.	400.
RBSQ	1.	1.
RBFR	80.	80.
QA	30.	20.
ROUTB	50.	50.
ROUTC	10.	10.
QB	30.	20.
APPOS	.1	.1

			#5 of p. 49 Bk 4	#1	#7
k_1 = RACT*RBSQ	600.	400.	500.	500.	500.
k_2 = RACT*RBFR	48×10^3	32×10^3	4×10^4	4×10^4	4×10^4
k_3 = ROUTB	50.	50.	50.	20.	50.
k_4 = QB/QA	1.	1.	1.	2.7	2.
k_5 = QA/RACT	.05	.05	.05	.03	.05
k_6 = ROUTC	10.	10.	10.	5.	10.
$\frac{k_6}{k_3 k_5} = \frac{E_{ss}}{g_{ss}}$ for J small $\left(\frac{RACT}{QA}\right)\left(\frac{ROUTC}{ROUTB}\right)$	4	4	4	~8	4
$\frac{k_6}{k_4 k_5} = E_{ss}$ for gain $\left(\frac{RACT}{QB}\right)\left(\frac{ROUTC}{.05}\right)$	200	200	200	~60	100
$\frac{k_2 k_5}{k_6} \times g_{ss}$ for V=1 $\frac{RBFR \cdot QA}{ROUTC}$	240	160	200	240	200

9/23/64 Review kinetic constants while waiting for recompile of new programs.

New 93C + 94C compiled OK.

Bad 795C + 95C had small errors

Now also necessary to recompile 794C to make compatible with 93C & 94C

Page ~~20~~ of Book 4:

	Hot	Cool	Try Hot	Med.	Cool
RACT	600.	400.	600.	500.	400.
RBSQ	1.	1.	1.	1.	1.
RBFR	80.	80.	100.	80.	75.
QA	25.	20.	30. 20.	25.	20.
RouTB	40.	50. → (35.) 40	40.	40.	40.
RouTC	10.	10.	7.5	7.5	7.5
QB	25. increase	20.	60.	50.	40.
AFPOS	.1	.1	.1	.1	.1
	e.g. .8841	eg. .8741			

k_1	600.	400.	600.	500.	400.
k_2	48×10^3	32×10^3	6×10^4	4×10^4	3×10^4
k_3	40.	35.	40.	40.	40.
k_4	1.	1.	2. -3.	2.	2.
k_5	.0416	.0875	.05 .033	.05	.05
k_6	10.	10.	7.5	7.5	7.5

Note that QB could be doubled.

ROUTC can be reduced

~~to~~ fit the earlier good Combinations.

for longer refract period use ROUTC = 5.

Extracellular Sequence

KVE=1 VE with zero shunt conductance

KVE=2 (with shunt factor but without pot. divider
this can be skipped by using 0 in the hundreds
digit of IFVE

KVE=3 includes effect of conical resistance

KVE=4 Superimposes potential divider effect.

IFVE = 2222 means compute, tabulate + plot all four stages

= 1001 means compute and tabulate only 1st + last stage

Could increase VEF

9/28/64 Review The new runs.

64795.9001 & 2 & 3 revealed trouble in Subroutine Argument

64795.9004 successful with hot kinetics & active dendrites, NSD = 5
5 But trouble with XNSD in Subroutine WXR95C

soma peak at	periph peak
KT = 23	KT = 24
22	23

This showed that RSOK = 1.2 made soma spike peak occur only one KT ~~step~~ sooner.

In both cases the dendritic spike was nearly synchronous

These are without BEB

	soma	dendritic			
I.C. =	.25	.2	.15	.1	.05
Kinetic counts.	600.,	1.,	100.,	25.,	40., 7.5, 50., 0.1

64795.9006 (9/25/64) first completely successful full extracellular run

same kinetics as above, but with I.C. = .3, .25, .2, .1, 0, 0

soma peak at	periph peak
KT = 17	KT = 19

The extracellulars are acceptable, but
neg peak amplitude = -1.2
pos peak 0.8

KT = 22 The time of the surface neg. does
coincide with inflection point of the
intracellular spike at soma, rather
KT = 19 than peak of periph intracellular

This fits the time derivative interp. of the differencing between two electrodes.

rel. to Jose's question

9/28/64

64795.9007 (9/25/64) same as .9006 except that RSOK = 1.5

some peaks KT = 15 — some peak KT = 17 — compared with 17 & 19

also skipping shunt current & core resistance worked.

Then, on 9/25/64 set up (64795.9008, 9, 10, 11 and 64794.8855) ⇒ to get active & passive with NJD = 5 & 10

Important Changes: Reduced ROUTC to 5.

Also made "cooler" kinetics for 10 & 11 active

with 400., 1., 75., 20., 40., 5., 40., .1 cool

whereas hot 600., 1., 100., 25., 40., 5., 50., .1 hot

But noticed that so-called cooler kinetics did not propagate more slowly

i.e. took longer for spike to reach peak in first axonal segment, but then prop. as well!

perhaps because larger area of spike provides better feeding of next cpt.

cpt 9
KT=31
ampl .475

29
.474

K= 12, 14, 07, 39
.915, .918, .865, .927

looks as though it would reflect

9/28/64

64795.9008 passive dendrites hot kinetics, NJD = 5

peak Gsto	.1	2	3	4
KT	6	9	12	23
ampl	.941	.942	.930	.787

This run is good enough for a complete run. NT = 81 (see p.)

However, can also explore with ⓐ less I.C. + E ↑ perhaps flat 0.1 for some & d + B = 0.05 for " "

KT	6	9 .9021	11	22
ampl	.942	.945	.930	.794

negligible difference.

ⓑ Could double RBSQ

ⓑ another with B = 0.1

ⓒ another without stimulus to check background.

64795.9009 same with NJD = 10

KT = 6, 10, 13, >41 got too much soma delay
.934, .934, .916, ?

needs more oomph
6, 9, 12, 41 try above. RBSP = 2

64795.9010 active dendrites with cool kinetics NJD = 5 got synchronous dendritic spike

KT = 10, 13, 16, 32 & peak 32
.909, .909, .857, .939 .951

← 64795.9011 same with NJD = 10
soma delay too long.

Redo 22, 23 & 24 with NT=51 altogether.

9/28/64

Setup 64795.9015 passive same as .9008 with IFTEST=0
IFVE=2000 ~~112~~
NPLT=3
NG=2
NT=81

Time Est.
~~150 225~~ ~300 313

116 ~~150~~ 140 64795.9021 NT=61 RBSQ=2. IFVE=1000
OK but negligible difference IFTEST=1103111

116 ~~150~~ 140 .9022 RBSQ=1., but NES=1 & B=.05 in S&D
lost BEB ∴ blocked I.C.=.1 in S&D

117 ~~150~~ 140 .9023 " " same with B=.1 in S&D

did not run because of error 130 .9024 same as .9023 without I.C. in axon. as a control.

above all for NSD=5
following for NSD=10

Actual 176 200 .9025 NT=81, RBSQ=2., I.C. as in .9009

200 .9026 RBSQ=1., NES=1 & B=.05 in S&D
I.C.=.1 in S&D

200 .9027 same except B=.1 in S&D.

200 .9028 control with zero I.C. in axon

active

240 .9029 similar to .9011 but with
NT=81, NES=1, B=.05, .04, .03, .02, .01

production
60/1040
17

70 pages

Problem 64795.9015 revealed error at statement 691 of WXR95C which affects only the CONE calc for passive dendrites & was not previously tested. This now being fixed together with minor change at 743 to be explicit about skipping shunt factor whenever stripped. This error discovery justifies the caution in setting up .9015 as less than a full run, (as originally intended).

We can now judge if NT=81 is too much.

perhaps not.

64795.9021 RBSQ=2. made very little difference
one KT earlier in yts. 3 & 4
∴ Might even try RBSQ=5.

.9022-24 blocked because BEB input card was incorrect

similar trouble with .9026-28

need rerun

Run time →
estimated at 100 secs
was 100 secs

Principal difference is that both B&C grow faster with RBSQ=5. & hence reach peak conditions sooner in Cpt. 4. Difference presumably not enough in Cpt. 3 (because safety factor is greater. The actual peak coolers in Cpt 4 (& different KT) are very similar.)

10/1/64 (set up 9/30/64)

64795.9031 RBSQ=5. otherwise like .9021 & .9008

Here ~~peaks~~ in cpts	1	2	3	4	9
KT	6	9	11	19	26
	.942	.945	.938	.807	.468

Soma spike is earlier, cf. p. 14, whereas cpts 1, 2 & ~~3~~ are same 3 very slight.

64795.9032 and .9033 SNAFU because neglected to set NEJ=1

It is very interesting that increasing RBSQ from 1. to 5. had no essential effect upon axonal propagation, but significant effect upon soma delay. Now look at B & C values

.9021

	cpt 3	cpt. 4
KT=11	.9301	.3328
	.7005	.0207
	.3499	.0225
KT=15	.5991	.4582
	.1741	.0655
	2.7301	.0794
KT=22		.7941
		.4572
		1.0257

.9031

	cpt. 3	cpt. 4
KT=11	.9375	.3801
	.8927	.0374
	.6509	.0384
KT=15	.4851	.5969
	.0933	.1619
	2.9099	.1702
KT=19		.8071
		.5080
		1.0258

		Estimated	Actual
Estimated Runtime	.9016	380	390
	.9035	380	346
	.9036	180	163
	.9037	180	163
	.9039	380	418
		1500 secs	
		or 25 min	

Actual runtime was (1485 secs)

or 25 min

letter not put
BEB and Sonia

10/1/64 (set up 9/30/64 production run)

64795.9016 Intracellular is fine.
SNAFU with CONE
Could it be that they did not have the new version of 95C incorporated into their production run?

64795.9035 RBSQ = 5. passive NSD = 10
compare with .9025

	.9025				.9035			
Cpts.	1	2	3 & 4		1	2	3	4
KT	6	9	12	41	6	9	12	30
	.937	.936	.918	.756	.940	.942	.923	.7786
eff. 14	KT = 56, ampl. .270				KT = 45, ampl = .274			

∴ prefer RBSQ = 5.

~~Still~~ Here also trouble with 95C CORE

64795.9036 blocked, but might have been OK. with RBSQ = 5. ?

64795.9037 good with BEB = 0.1 did not block
Some peaks @ KT = 30, ampl .6765

eff. 14 @ KT = 48, ampl = .246

10/1/64

64 795.9039 / actnie with NJD = 10
cooler kinetics.

Note (1) Here Cone calc. works!
permBdy became active

(2) also BEB was for too effective
reduce I.C. & maybe make flat
also, might as well use RBSφ=5.

Encouragement to use flat facilitation
certainly for passive, but
perhaps even for active.

10/1/64

Comparing NJD = 5 & 10

True distance from soma to glom ≈ 0.4 mm.

∴ when NJD = 5, compartmental $\Delta X = 0.08_{mm} = 80\mu$

when NJD = 10, compartmental $\Delta X = 40\mu$

We have been assuming that ΔX is same for axon & dendrites and thus $\frac{UA}{UD} = \frac{\text{axon diam}}{\text{dend. diam.}}$

If $\Delta X = 40\mu$ and axon diam = 2μ, surface area of one axonal compartment is about $240\mu^2$

If $\Delta X = 80\mu$ ——— get $480\mu^2$

Soma surface area approx that of cube 20μ on side

get $6 \times 20^2 = 2400\mu^2$

∴ when NJD = 10, $\frac{C_A}{C_S} \approx \frac{1}{10}$ ∴ here $\frac{USA}{UA}$ should be $\frac{1}{10}$

when NJD = 5, $\frac{C_A}{C_S} = \frac{1}{5}$ $\frac{USA}{UA}$ should be $\frac{1}{5}$

Recently, have used $\frac{USA}{UA} = \frac{5}{25} = \frac{1}{5}$ / but should use USA = 2.5 USD = 100. for a ratio of 40

Whereas for UA=25 home $\alpha \frac{USD}{USA} = 40$

	UA	UD	USA	USD
NJD=5	25.	100.	5.	200.
NJD=10	25.	100.	2.5	100.

10/1/64

Conclusions, might wish to try

$$\frac{UA}{UD} = \frac{1}{3} \quad \sout{\text{e.g. } UA} \quad \frac{33}{100}$$

look back at page 70 of Book 4 $\frac{USD}{USA}$

Consider minimum dendrites as 1 primary + 2 sec.
with diameters approx 3 times axon..

then $\frac{USD}{USA} = 3 \times (3)^2 = 27.$

Consider one primary with diam ratio = 4
~~3~~ 4 sec. 2

$$\text{e.g. } 16 + \sout{3}\, 2\times4 (2)^2 = \sout{28}\ 24$$

$$16 + 4(2)^2 \quad 32$$

---

all runs have UD = 100

∴ we could do some runs with UA = 33

& $\frac{USD}{USA} = 25$

		UA	UD	USA	USD
for NJD = 5	this means	35.	100.	7.	175.
for NJD = 10		35.	100.	3.5	88.

Computer Time on Production Run

	Rough Est.	Actual	Cum
9041	118	110	
9042	118	111	221
9043	112	104	325
9044	120	116	441
9045	200	219	660
9046	100	114	774
~~8046~~	100	113	887
9047	100	109	996
8048	(263) added	~~278~~	~~1274~~ 1273
9048	263	278	1551
9049	263	277	1828
	1757	1828	

10/2/64 Quick overview of new results.

64795.9041 flat residual facil worked fine. .3
? ~~preferable~~ to .9031 (where soma spike onset is more gradual
soma peak = 81 Possible with NSD = 5, with no E

Also cone now working, evidently previous series had not used the new 95C

Good extracellular series — suitable for plot.

64795.9042 flat residual facil 0.1 plus B = .05
hillock peak at KT = 11
soma " KT = 35
} longish delay
soma peak 75

possible for use: did not reflect.
but next case is probably better.

64795.9043 same as done with B = .1

good run.

But may need controls to see if 41 & 43 would fire without antidromic.

Ideal may lie between 42 & 43

Next run could be like 43 without E in soma

do Norbert for this

afraid that these would fire without antidromic

These all used facil removed from soma

10/2/64

64795.9044 active, "cool", short flat mild facilitation (both residual & B)

got synchronous soma dendritic with "good" axon-soma delay.

Extracellular is lobe $\frac{dV}{dt}$ & amplitude is only 0.2 mV. for VEF = 4.

down a factor of about 10 from non-synchronous dendritic spike.

of interest for Stefanis Story

We cannot rule out VEF = 40. apriori, but it can probably be ruled out on the basis that E & J can modify microsoon such that synchrony would not always obtain. ?

Any variation in synchrony would have severe effect on amplitude.

Also, delay of of neg peak with distance may be diagonistic etc. — should be checked.

64795.9045 passive NJD = 10
USA = 2.5 USD = 100.
flat residual facil. = .25 in dendrites
but not soma

soma fired at KT = 18

good run
it is clear that residual fail was decaying
& would ~~not~~ likely ~~probably~~ fired without antidromic
see p. 32
amplitude decrements to 0.25 in pt. 14

Should plot
excellent, but
check control without antidromic.

~~pos spike~~
pos peak of period II at soma
is very slow, ampl ≈ 1/4
of neg peak
in Period I

64795.9046 passive as above
but with B = .05 in dendrites
I.C = .1 in soma & dendrites
soma fired at KT = 43

64795.8046 same as 9046 except that USD = 62.5

here soma fires at KT = 27

64795.9047 like .9046 except B = 0.1 in dendrites

here soma fired at KT = 39

*

provided not too steep

The problem of minimum amplitude proximal to glomerulus may be resolved or avoided by the primary & secondary smearing which will make periphery necessarily have lower amplitude.

A contra-indication for the active syndrome case is the very small peak amplitude at intermediate depths.

~~Cons~~ Consequences of synchrony

1. small amplitude of extracell
2. faster fall of intracellular
3. more nearly equal size of + & − peaks (as expected for dV/dt)
4. get minimal amplitude at intermediate depths.

? Must discover basic cause of dip, because it may occur also when passive

(it is a cancellation due to PD effect)

? phase

10/2/64 Active with NJD=10
"cool" kinetics

64995.8048 USD=62.5 flat facilitation
I.C. = 0.1 S&D
B = .01 in Donly

Soma fires at KT = 24
cpt. 14 25

nearly synchronous

expect $\frac{dV}{dt}$ approx for Ve KT=22 ampl = -.54
for VEF = 4.

Might pay to try to slow falling phase
Because falling phase is not counteracted by electrotonic back flow from a later downstream spike, since here spike is synchronous.

64795.9048 same as 8048 with USD=100.

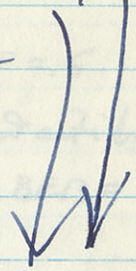
almost synchronous
Soma fires at KT = 24
cpt. 14 at KT = 25
trivially different from .8048

64795.9049 had I.C. flat, but B values graded (similar to .9039) but better
Here dendritic invasion is progressive

Presumably soma would fire without the antidromic. This needs to have E taken out of soma

10/2/64

Could do a ~~sequel~~ to ~~64794.8214~~ for granule cell with
RHOSOM = 1.0
RHOGLM = 1.6



See 8215
9/15/64

Use VEF = 10./5.

DT = .01
NSTEP = 5
NT = 70

RSOK = 1.0
needs card 6

8216
9/16/64

10/5/64 Set up production runs

	est. time
~~64~~ 795.9051	116
52	90
53	116
54	90
55	90
57	260
58	260
59	277
	1299
.8217	300
.8218	300
	1900
60	31.3

I.C. = 0.2, PDF = .5

control without antidromic

I.C. = 0.1 with BEB = .1

control

control on 45

same as 58 with BJC for decrement

Same as 48 with QB reduced

" " 59 with some BEB deleted.

Actual run time was 1994 secs

note that extracellular pots. are essentially the same for this as for antidromic →

10/6/64 Looking over results of production run

64795.9051 Passive, NJD=5, hot, I.C. = 0.2 flat in dendrites but not soma, NEJ=0

soma peak occurs at KT=32

(in .9041 " " " " KT=16, probably would but might have fired without the antidromic.

May work to increase I.C. to 0.25

intracellular peak amplitudes cpt. 4 5 6 7 8 9

.77 .64 .55 .49 .47 .46

The extracellular pots. are not pretty enough; maybe this reaction is mainly to the delay, but period II is rather blunted.

64795.9052 control with I.C. = 0 in cpt. (1).

soma fired at KT=38

hillock fired at KT=27

(1) We may have to tolerate a low level of spontaneous firing. However, exp less than 10 per sec.

(2) RBSQ may have to be set back from 5. to 1., but this may require more residual facil. to prevent antidromic block.

(3) Perhaps initial conditions needs to include some refractory BTC in the axonal & soma cpts.

10/6/64

One implication is that, with passive dendrites, a soma spike does have significant electrotonic spread into the dendrites, but the dendrites do not actively "clear" themselves & residual facil. is temporarily enhanced (which may not fit physiological facts? i.e. dendrites are facil. (depol.) but are the soma & hillock refractory?)

Important to follow the recovery of soma and hillock BEB + BJC after firing to see how refractory & also to see how much soma repolarization does to clear the dendrites?

64795.9054

Control got local resp leading to peaks at KT=42 in Cpts 1+2
KT=44 in Cpt. 3
~~KT=48~~

~~Which~~

Cpt. 3 got ahead of cpt. 4 @ KT=25

Could make $U_{AS} = 2. * U_A$; $U_{DS} = 2. * U_D$

and make $U_{SA} = U_{AS} * \frac{C_A}{C_S}$; $U_{SD} = U_{DS} * \frac{C_D}{C_S}$

10/6/64

64795.9053 passive, NSD=5, hot, I.C=.1 S+D
BEB=.1 in D only.

← Control 54

soma blocked

peak was .1702 @ KT=15+16

previously 42+43 had BEB in the soma + did not block but suspect would have fired without antidromic

notice $\frac{USA}{UA} = \frac{5.}{25.}$ USS = 206.

Note that UA=25. means that $\Delta Z = \frac{1}{5}$

$\therefore R_{i\Delta Z} = \frac{1}{5}(ri\,\lambda)$ while $R_{m\Delta Z} = 5\left(\frac{rm}{\lambda}\right)$

or $R_{m\Delta Z} = 25\, R_{i\Delta Z}$

or $g_{A_0} = \frac{1}{25} g_{A_{ij}}$

or $U_{A_0} = \frac{1}{25} U_{A_{ij}}$

or $U_{A_{ij}} = 25\, U_{A_0}$

Now, we assume $g_{SA} = g_{AS} = g_{A_{ij}}$

Intuitive explanation of soma block is that the rate of electrotonic spread into the dendrites is rapid. Therefore depolarizing current from bitor must buck the loss of soma to rapid equalization tendency. As USD and UD are increased to larger values, the soma capacity is

Compare 64794.8853 & 4 (9/22/64)

where USA=10. & USD=400.
gave longer axon-soma delay
than USA=5. & USD=200.

everything else the same

However these dendrites were active,
may need to be rechecked with passive dendrites

in this case, the key to the difference is that the soma had a large I.C. and lost it less rapidly (because of larger C, smaller USA & USD) than in 53
& this setup an earlier soma local response & earlier soma firing in spite of weaker feed from butter.

placed more & more instantaneously in parallel with the dendritic capacities & it becomes less & less responsive to depolarizing current. Also any brief ~~excess~~ of soma depol over dendritic depol. disappears very rapidly.

Also, the amount of current flowing into the soma as a consequence of hillock spike is proportional to USA.

∴ Doubling USA doubles current into soma.
but Doubling USD doubles tendency of soma to equalize with the dendrites.
The net result is less sensitive soma response.

Note: p. 24 64795.8046, decreasing USD only caused soma to fire sooner for case of passive dendrites. Because exchange rate with dendritic load was reduced, i.e. soma was less sluggish.

but, p. 25 64795.8048, decreased USD had very little effect when dendrites were active.

64795.9054 – Control for 53 (see p. 30 & opposite.

This shows that it is possible to have spontaneous firing of hillock & axon without firing of the soma. The soma just sees depoll. up to 0.2

~~#~~ impulse arises at cpts 1+2, say at first node.

64795.9055 Persone, NJD=10
Control for 9045
without antidromic

~~Soma fired at KT=~~

peaks	cpts. 1	2	3	4
KT =	13	14	16	19
Use as for .9045	6	9	11	18

64795.9057 active NJD=10
attempt at decremental story
blocked at soma.

BJC = .1, .2, ... -1.0
cpts 5 6 . . . . . -14

6715, 7053 — Control for 53 (see p. 30 of diary)

This stamp Tr 7 is possible to have Mr. Thompson's of Water & Power write out first of all. The stamp just reads depot. up to 0.2

10/6/64

64795.9058 active, NJD = 10, cool kinetics QB = ~~30~~ 20.
I.C. = 0.1 in S&D
BEB = 0.01 " " " "

Compare with 9048 (p. 25) where QB = ~~40~~ 40.
Same synchronous spike at KT = 24, 25
very small extracell.

64795.9059 active, NJD = 10, cool kinetics QB = 40.
~~shaped I.C. to~~
flat residual fail
shaped BEB same as 9049 except here not in soma.

---

pretty good extracellulars
but (a) does special shaping
(b) would fire from shaping alone

would be suitable for plotting, except would take fall of intracellular to be slower.

See below get, if half of the mitral cells fire:

$\frac{VEF}{100} = \frac{1}{14}$ for $Re = Ri$ i.e. .07

get $\approx \frac{4}{14} \approx \frac{1}{3.5}$ for $Re = 4Ri$ i.e. ~~0.285~~ ≈ .3

Suited for passive decrements or slow activation with significant SHUNT current.

Suited for nearly synchronous dendritic spike

Suited for passive decrements

alternatively could take an $Re = 50 \Omega cm$ and estimate true extracellular crossect. which however would be something like ?

note granule cell dendrites & axons which lie parallel to mitral dendrites will, if they are several λ long, will be open to current flow between mit. level & glomerular level.

Thus we might approach $\frac{Re}{Ae} \parallel \frac{Ri}{Ai} = \frac{Ai}{Ae} = \frac{100}{800-100} = \frac{1}{7}$ assuming that all mitral cells fire

10/6/64

64795.8217
.8218

granule cell series.

pretty good sums

get surprisingly sharp reversal of extracellular in gyr-S

$$\frac{VEE}{100} = \frac{re}{ri} = \frac{Re/Ae}{Ri/Ai} = \frac{250/800\mu^2}{50/(5\times30)\mu^2 \text{ per cell}} = \frac{5\times150}{800} = \frac{750}{800} \approx 1$$

1200 mitral cells per $mm^2 = 10^6 \mu^2$

$\therefore$ each has $Ae \approx 800\mu^2 - Ai$

full crossed Re effective

alternative $(3\times30) = 90$ get $\approx \frac{1}{2}$

$Ai \simeq 100\mu^2$

$Ae \simeq 800 - 100 = 700$

$$\therefore \frac{Re}{Ri}\frac{Ai}{Ae} = 5\left(\frac{1}{7}\right) = \frac{5}{7}$$

Suppose only every other mitral cell fires, then $Ae \approx 1600\mu^2 - Ai$

then get $5\left(\frac{1}{16}\right) \approx \frac{1}{3}$

Gordon volleys were often slightly less than maximal; however, it is possible that a substantial fraction of the mitral cell population blocks at the sound, perhaps not the same cells on each test. Presumably there is graded dist. of safety factor.

looked at 64795.9058
pt. 10
where neg peak amplitude was -.02

but some neg peak amplitudes were -.41

would need

VEF ≈ 5×4 = 20.

If previous para is correct, we can justify VEP values as large as 10. to 50., which means that the almost synchronous dendritic spikes would have $\frac{dV}{dt}$ extracellulars of sufficient amplitude to agree with experiment.

Must re-examine such cases of active dendrites.

Raised question as to whether facil can result from ~~Volley~~ previous volley (usually 1 sec) earlier.

Inhib. usually lasts $\approx \frac{1}{2}$ sec but found only in about half the cells

---

Period I seems to require the potential divider. works equally well for active & passive. effect.

Period II should have a reversal point of rather small neg.; if it were due to initial GEC only.

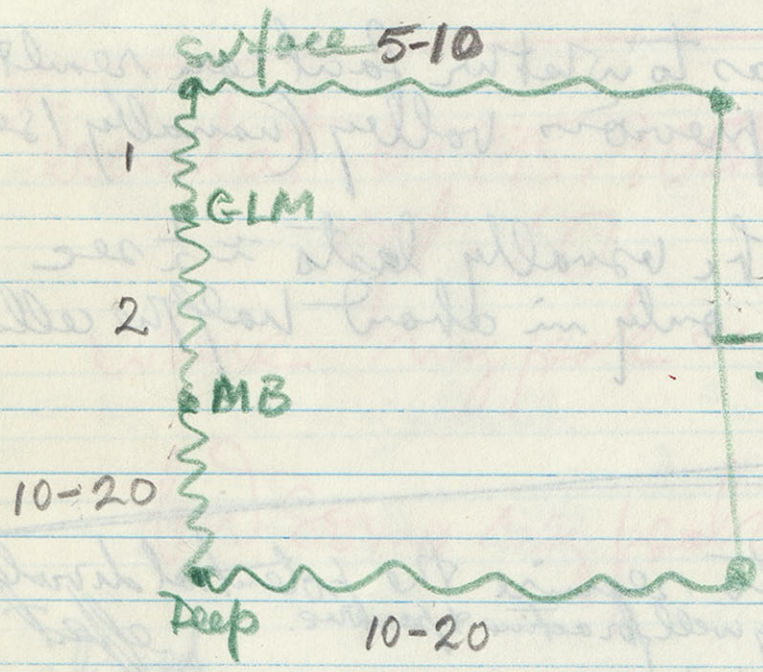
~~However, Period II has a durable~~

However, The intermediate triphasic record has a prominent negativity which is hard to duplicate with initial GEC alone (i.e. with nearly synchronous active dendrites)

Probably need to use deep apical GEC to take care of this!

$$SHCF = \frac{2}{25\text{-}50}$$

$$\approx \frac{1}{10} \text{ to } \frac{1}{20}$$



$$\therefore \frac{R_{gl\text{-}gd}}{R_{MB\text{-}gd}} = \frac{6 \text{ to } 11}{20 \text{ to } 40} = \frac{1}{2} \text{ to } \frac{1}{7}$$

see p 87 (85) of book 4

$$\frac{R_{surf\text{-}gd}}{R_{mb\text{-}gd}} = \frac{5 \text{ to } 10}{(5 \text{ to } 10)+3} = \frac{5}{8} \text{ to } \frac{10}{13}$$

$$\frac{1}{2} \text{ to } \frac{3}{4}$$

$\frac{6}{8}$ to $\frac{11}{13}$ $\frac{3}{4}$ to $\frac{5}{6}$

10/6/64

Even the passive dendrite case has trouble with the amplitude of negativity in the transitional triphasic.

Here again, need deep ayon GEC

This serves two purposes

① it shaves surface pos. of Period I to make the peak ~~sooo~~ be earlier.

② it provides robustness of the transitional triphasic.

10/6/64 Ponder the transitional triphasor

See next page

10/7/64

Tonsinic deep ayon GEC get a soma spike with little or no dendritic invasion, by shunting. UD very small.

This criticism applies primarily to the synchronous active dendrites.

In particular, the stupid active .9059, has a very prominent negative peak in its transitional trophase.

What are the discrepancies of using Mitral GEC only.

(1) Period I surface + peaks a little earlier than deep neg.

(2) ~~Period~~ Theoretical Transitional triphasic has a negativity (Goes in depth + in time) that is too small (because of PD cancelling effect) ~~red to surface neg.~~

(3) Period II Experimental surface neg tends to be larger in abs value than the surface pos. of Period I, ~~Period~~ while deep pos of Period II is smaller than deep neg of Period I!

Whereas Theoretical, for passive dendrites has a much smaller surface neg. in Period II.

For active dendrites, depends upon details of $\frac{dV_i}{dt}$.

10/7/64 plot best ~~calculations~~ computations now available 38

64795.

Done 10/7/64 10/8/64

passive NJD=10, probably best is .9045
of. ~~.8046~~ no extracellular

active NJD=10, .9058 ~~of~~ .9059 64791
flat shaped also old 0669

short passive NJD=5 .9041 64791
also old 0666

short active NJD=5 .9044
essentially synchronous

another short active NJD=5 .9006
some peaked KT=17, periph peaks at KT=19

10/8/64

.9041 slightly better short passive than .0666

.9069 { .9059 and .0669 shaped active long
These both have the most prominent transitional triphasic. They will be superseded by .9069 with QB=30.

(peak neg.
−.22 with VEF=4. .9044 is best case for synchronous active dendrites
−.414 with VEF=4. .9058 is good for showing problems of " " " "
−.78 with VEF=3. .9006 is O.K. but adds nothing to the other two except note amplitude factors here.

.9045 is a good long passive, less sharp but slower than .9041

May wish to plot

latency versus distance of intracellular peak
extracellular crossover
" peak neg.

Use time of histoc intracellular peak as zero.
or possibly time of cpt. 1 peak

did this 10/8/64

Plan to run 64795.9069 like 9059
but with QB = 30

64795.9062 like 9052 control but with
~~IFTEST = 15 or 10?? 15~~
~~and with~~ NT
if I would 250 ~~Times~~ values to cover 2.5 T
~~IFTEST~~ = 125120 Then each DT = .01

NT = 251 all else same as before
except IFVE = 0 & delete card 6

approx 550 sec

64795.9064 like 9054 except that
KTB = 251

approx 580 secs

NT = 251
IFTEST = 125120
IFVE = 0, delete card 6

	est.	Actual
.9061	140 sec	
.9062	550	
.9063	550	
.9064	140	
.9065	140	
.9066	140	
.9067	550	
.9068	550	
.9069	280	
.9070	280	

60 | 3320 sec

55.4 min.

10/9/64

Also do an active & a passive with VEF = 6.
SHCF = 0.5
PDF = 0.25

to see what happens

Try this with .9061 based on .9041 VEF = 12.
.9064 based on .9044 use VEF = 40.

.9066 based upon .9057 for decremental spike

.9069 like .9059 but with QB = 30, 20;

.9067 controls for active case NSD = 5 based on 9064
.9068 "

Best ones for plotting

.9045 passive, long Z, flat facil.

.9041 passive, short Z, flat facil.

.9059 active, long Z, shaped facil. (large + phase)

.9044 active, short Z, flat facil.

Consider rerun with different VEF

.9045

		ampl in (4)
~~(1) KT=~~		
(2)	KT = 14	peak = -.9163
(3)	KT = ~~23~~	= .80
(4)	KT = 25	+.06
(5)	KT = 27	+.33
(6)	KT = 36	+.60
(7)	KT = 51	+.43

.9041

KT	ampl in (4)
~~10~~ (11 better)	~~-.53~~ -.608
15	-1.39
19	-.79
~~21~~ (22)	~~-.07~~ -.08
23	.27
28	.55
37	

and DT = .005

10/9/64 Gradient plots.

pick KT values, such that M.D. level spike (with PD effect) is

~~(1) 1/10 or 1/5 of peak ampl.~~

(1) (2) 1/2 of peak ampl.

(2) (3) peak neg.

(3) (4) 1/2 back

(4) (5) crossover

(5) (6) 1/2 to pos. peak

(6) (7) pos. peak

(7) (8) 2/3 recovery

(3) 4 ~~5 6 7 8~~ → 9 5 steps

(2 3) 4 5 6 7 8 9 10 11 12 13 14 10 steps.

also .9044 should be spread out.

Review

64795.9061 passive based on 9041 but with VEF = 12., (SHCF = .5) O.K.

.9062 NT = 251 passive control spont. act. exp. in axonal cpts., soma does not fire second time

.9063 passive similar but with BEB = 0.1 in dendrites

~~KT~~ = 42 axonal firing without soma
KT = 100 soma fires first
KT = 222 axonal ~~firing~~ without soma
KT > 251 looks like soma will fire first.

.9064 active, erroneous input cards
should redo correctly.?

have soma & dendrites fired before ~~soma~~ axon become of BJC made fail

.9065 active decremental conduction case needs more I.C. ~~&~~ BEB } delay too long.

.9066 Better, but not enough decrement.
need larger steps of BJC

.9067 active control with NT = 251 & ~~two~~ NES

KT = 1 and 199

soma dend. fire at KT = 7 ← against 106 ←

Then all damped out

.9068 active control with NEJ = 0
soma dend fire at KT = 19
beyond KT = 210, seem to get an artefactual beginning of local response

.9069 active ~~redo~~ of .9059 with QB = 30.
This showed peripheral dendritic spike larger than other dend.

.9070
QB = 20.

+questions of complex frequency domain of transfer fcns.

10/19/64 past week was lost to referee work etc.
However 10/9/64 - 10/12/64 saw the plotting, with Mr Gordon, of a set of transients and gradient plots suitable for final paper. This week is Gordon's last week before leaving for Stockholm. He is working on part of the manuscript, and right now, I will set up the last few computations that we can study together.

The long time calculations revealed that there may be a minor problem at 455 and 462 of WXR93C & 94C which prevent B value from going all the way to zero. This was noted 10/12/64 and we hereby plan to correct this and retest.

Also 451 and 452

Modify WXR 93C into WXR 96C
94C 97C
795C 796C

Compare

	QB=40.	QB=30.	QB=20.
KVE=4	.9059	.9069	.9070
VE neg peak pt.4	-2.1031	-.2.1132	-2.1402
pos peak	+2.3687 1.13	+.2.3272 1.10	+2.2014 <1.03
intracell peak in (10)	.9217	.9294	.9370
(14)	.9570 1.04	.9603 1.03	.9631 <1.03

Will have to carefully check status of the figures.

Wednesday: Today Gordon is in Boston; he will leave at end of the week. Today I will make a concentrated study of the rough draft as it stands, in order for us to be able to discuss it before he goes.

Sept. 24

I had previously gone over the text written around figs 1, 2, 3, 4. The new material is written around fig. 5. Return to Beginning now.

Fig. 1 1-A is exp. set up diagram
1-B is anatomical schematic diagram

p. I-A 1.1 distort for indifferent
? "initial" response
(resistive) location of the distant electrode on this current pathway...
These impulses travel antidromically...

p. I-B 1.2 revise according to note A, as follows
When, for example, the peak of the impulse is at the (soma) mitral body (point C in Fig. 1-B), ~~current~~ the soma membrane depolarization is associated with a soma interior whose potential is more positive than all other regions of the mitral cell interior;
(therefore) current must flow (intracellularly) from the soma into the dendrites; this current flows out across the dendritic membrane, and then it must flow (extracellularly) from the dendritic regions (A and B of Fig 1-B) back to the soma at C.

Consider whether we need the term, initial GEC, here?

10/24/64

1.3
p. I-3 ? Gordon's ? about granule neg etc at bottom

2.1
p. II-1 mitral bodies, not apon bottom.
? full series where?

p. II-2
2.2 triphasic (+-+), with its negative peak near the time of transition from Period I to Period II.

avoid mirror image: are of opposite sign, but otherwise similar in time course. As will be discussed later, the deviation from precise proportionality can be attributed to activity in cells other than the mitral cells.

We will show that the surface negativity of period II can be regarded as a sign of soma membrane depolarization rather than of impulse arrival at the periphery.
(but Gordon lost this emphasis at 5-g ≡ V-7)

Fig. 3 was to be exp. gradient plots. But this led to numerous difficulties in pages 3.1 + 3.2
Decided to skip these problems until later

~~Draw Fig. 3~~
The figure number gained can be used to include the full experimental series as Fig. 2 or 3.

~~Plane projection~~ The apex of the cone, as shown in plane projection in Fig. 4 should really be an angle of only one or two degrees.

p. 34 gives $A = 800\mu^2$ at initial cell level $\approx \rho = 1.3$ mm $= 1300\mu$

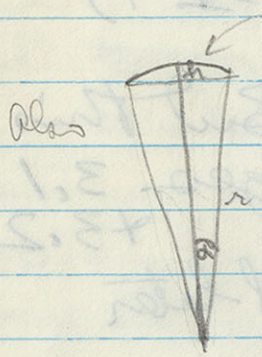
$800 = \pi a^2$
$a = \sqrt{255} \approx 16$

total surface area of a sphere is $4\pi\rho^2$
$= (12.57)(1.69)\times 10^6\ \mu^2$
$=$

a whole sphere subtends 4π radians of solid angle

a cone subtends $\frac{800}{1.69\times 10^6} = 4.73\times 10^{-4}$ radians of solid angle

which is $\frac{4.73\times 10^{-4}}{12.57} = 0.376\times 10^{-4} = 3.76\times 10^{-5}$ of whole sphere



$r - h = r\cos\alpha$
$r\sin\alpha = \sqrt{r^2 - (r-h)^2}$

$a = \sqrt{800/\pi}$
$= \sqrt{255} \approx 16$

$A = \pi a^2$

for α very small, have approx $\alpha \approx \sin\alpha \approx \frac{a}{r} \approx \frac{\sqrt{A/\pi}}{r} \approx \frac{16}{1300} \approx 1.23\times 10^{-2}$

$2\alpha \approx 2.5\times 10^{-2}$ radians $= .025$ radians
$\approx 1°30'$

for every other cell, get $2\alpha \approx 3.5\times 10^{-2}$
$\approx 2°$

see next page

Page 4.1 dealing with Fig. 4 of cone model
Justification of cone can also rest upon my
separate paper.

* We could do a quick calculation of true cone solid angle size
ie. here the solid angle has been exaggerated.

Second ¶ of p. 4.1 might want to be turned around.
Also, should include possibilty that only half the
cells fire, but fairly uniform density of active cells.

dorsal & ventral layers not clear enough in center & then
"in through dorsal hemisphere & out through ventral
hemisphere" or something like that.

p. 4.2 footnote at bottom. ~~The model appropriate~~ ~~one~~ concession to ___ The model includes one
feature which corrects for departures from spherical
symmetry, otherwise, the simplication of spherical
symmetry is assumed. This one feature is an
external leakage path from the center to the
outside.

bottom ¶ confusion may result from
parsing - better treat each separately.

p. 4.3 ? confusion between current & resistance labelling.
are we using ind or dist?

from p. 34

1200 mitral cells per mm^2 seems to imply $\approx 25{,}000$ mitral cells per bulb, which is probably Gordon's starting point.

Solid angle of each cone $\Omega = \frac{4\pi}{N} = \frac{12.57}{25\times10^3} \approx 0.5\times10^{-3}$ radians of solid angle

for $N = 12.5\times10^3$ get $\approx 10^{-3}$ radians of solid angle

also, in radians, circular area for α small is $\pi\alpha^2$

$$\pi\alpha^2 = \frac{4\pi}{N} \quad \text{or} \quad \alpha = \frac{2}{\sqrt{N}}$$

$\therefore$ for $N = 25{,}000$, get $\alpha \simeq \frac{2}{1.6\times10^2} = 1.35\times10^{-2}$ radians
1.58
$= 0.77$ of a degree

for $N = 12{,}500$, get $\alpha = \frac{2}{1.12\times10^2} = 1.78\times10^{-2}$ radians
$\approx 1^\circ$

i.e. when half the mitral cells are active, ~~the effective~~ there are 12,500 cones each of whose elements of surface makes an angle of about 1° with the axis

$1^\circ = .01745$ radians

p. 4.4 ? axons do not (carry) inward ?.

If the reference electrode were placed at the dendritic periphery (A) instead of at DIST (or GD or ∞)

This explains the opposite polarity (or sign) of the potentials at (C) and (A) in Fig. 2

p. 5.1 ~~need only assume no~~
assume that there is no current through the external resistance loop, and that the reference electrode is at the same potential as if it were at the surface of the bulb or at the glomerular level (A).

p. 5.2 top ¶ no.
axon in oil; $\frac{\partial V_e}{\partial \rho} = \frac{-r_e}{r_i} \frac{\partial V_i}{\partial \rho}$

where r_e is a fcn of ρ

$$V_e = \int_{\rho=\Lambda}^{\rho=x} \frac{\partial V_e}{\partial \rho} d\rho$$

$$= \frac{-1}{r_i} \int_{\rho=\Lambda}^{\rho=x} r_e \frac{\partial V_i}{\partial \rho}$$

due to mitral gec ?

? ~~cos~~ cross section

$$V_{e2} - V_{e1} = \frac{I R_e}{\Omega} \int_{\rho_1}^{\rho_2} \frac{d\rho}{\rho^2}$$

p. 5.3 why use both r and ρ?
Better make a table for the paper.

pot. divides this way because same current flows all around & these are in series, and DIST represents (zero) reference point.

Give a numerical example: middle level (MBL)

Suppose Ve at MB is 2.5 mV neg. rel. to Ve at glomerular level (GL), then the 1:4 ratio of the resistances of external path means that MB is 2.0 mV neg rel. to DIST, while ~~DIST is 0.5 mV neg. rel. to GL~~ GL is 0.5 mV pos. rel to DIST.

GL to MBL

The amount of current will be 1/25 of that flowing within the cone from A to C, or 1/26 of the ~~total~~ current flowing from ~~the glomerular~~ A to C. GL to MBL.

maybe 5.5 should come first in the text, since it is the most important and has already been mentioned. The other two could go into fine print.

~~Two~~ seems to confuse surface record and glomerular level record.

Instead of ABC levels, Hovebord

Surf
Gl GL
D PL
MB MBL

p. 5.16 Perwood III ~~pre~~ depol. of soma membrane first & then pre passive electrotonic or active depol. of dendrites -

avoid source sink terminology

place emphasis upon current flow.

(It wouldn't matter if the soma were a source for axonal current flow, you would not see any pot. unless dendrites were also a source.

$G_\infty = \frac{1}{25}$ ∴ current flow due to Action Pot. voltage source is a negligible

i.e. have to consider the rel. amount of extracell. current generated.

may have to refer to a later discussion as to why the conventional interp of this pas. is incorrect because peripheral dentists are not sources, esp in case of .9045

p. 5.7 "It is misleading to say the the surface pos. of period I is due to the terminal dendrites acting as sources during soma invasion;"

It is due to pot. divider effect + soma neg. which is due to extracell. current flow from PL dendrites to MBL soma (but not exc. from periph. d.)

(look at the gradient plots to consider more carefully.)

confirmed

this provides a good transition

no, not simply a fraction.

Then all records would have exactly the same time course and differ only in magnitude or sign.

p. 6.1 characteristic length (λ)

l $\quad Z_L = l/\lambda$

I believe that elsewhere $X = x/\lambda$

∴ this X here is not consistent;

$X = x/\lambda$

$Z_i = \int_0^{x_i} \frac{dx}{\lambda}$ $\qquad L_i = l/\lambda = X_e$

$Z_L = Z_e$

But 1989 paper used L/λ

care in dealing with λ, R_m & R_i

actually better include also R_e

Discussion of Fig. 6 ÷ needs more emphasis upon positive aspects.

also, fact that facil needed to prevent block. also that dendrites firing last reverses ?

10/23/64 Windup Notes, esp. re figures

Fig. 2 – order photography of exp. series
11/5/64 to photog longest dimension (image) on print to be 9"

* Fig. 1-B modify on print, leaving out tufted & putting in collateral. Also GL, PL, MBL.
11/5/64 to photog

Whereas Fig. 2 will use words to designate layers.

Fig. 3 still needs to be prepared. (Gordon has done this 10/26/64) ✓
11/5/64 to photog

Fig. 4 W.R. finish this fig. after paper is completed.

* Fig. 5 3 records (Intra, Extra, Recorded)
Could be done before Gordon leaves.

Fig. 6 Probably replace 9059 (Four Theoretical Transient Series)
also 9041 & 9044 could have interpolated
smaller compartments.
Do new computations, plot with Dorothy & assemble.

Fig. 7 Latency versus Distance Plots.
These will be changed when 9059, 9041, 9044 are redone

I told Gordon that I would write the text for this section. He did have a start.

10/23/64

Fig. 8 Theoretical Gradient Plots.

See p. 41

? how to label times

Characterized by following points of the MBL theoret. transient.

I-a	early I	approx 1/2 of neg peak ampl (before peak)
I-b	peak I	approx peak neg.
I-c	late I	approx 1/2 back down
I-II	transition I-II	approx crossover
II-a	early II	approx 1/2 to pos peak
II-b	peak II	approx pos. peak
II-c	late II	approx 2/3 back down

need to redo Theoret with DT = .005 or smaller
possibly DT = .002 + tables only.

Fig. 9 Experimental gradient plots for comparison.

Use same seven points in time based upon the MBL record.

The range from surface (0) to 0.3 mm depth, Gordon says is not well documented. He kept moving the microelectrode in until he saw an obvious change. Thus, he did not document the very small changes between surface and GL.

These plots were done 10/23/64

Evidence against .9044 synch. dendrites with large VEF →

Because this has too large a deep gradient at early times

However, primary - secondary dendrite smear would reduce this!

10/26/64 Comparing gradient plots
Figs 8 & 9

Fig. 8 .9045, 9041, 9059, .9044

Fig. 9 prelim: Mar 30, Prod 2
May 16
May 2 (illustrative series)
April 12 Prod 3, less complete

General comments exp plots
we took 0.3 mm depth is negligibly different from surface ~~of then 0.~~
↳ this was time of Mar 30, Prod 2
but not of others.
May wish to plot only from GL.
Difficulty is that gradient from surface to GL was not fully documented. May include this in Stockholm series. But here, best start from GL to MBL to deeper.

Thaw II-a Time of Mar 30 Prod 2
of II-b of May 16
earlier records show small gradient for depths greater than MBL
but later records show large pos. slope near MBL
in some cases from MBL deeper
in others its Play to MBL
Small gradients can be explained by CORE ≈ 1/25
∴ large gradients cannot be due to mitral apons
& this is evidence for granule GEC. ‖ can lead to

May 31

Anterior Prod #1

I-a 1.5 msec depths	ampl.	I-b 1.8 msec
~~.46~~	-2 GL	-6
.70	-2	-12
.82	-4	-11
1.02	-16 MBL	-36
1.14	-25	-41

Posterior Prod #6

soft 0.7mm

depths	I-a 1.5 msec	I-b 1.8 msec
.25	+1	-2
.47	-1	-13
.56	-4	-22
.67	-12	-37
.76	-24	-41

Early gradients all agree on current flow from dendrites to soma.

Theoretical gave more indication of zero gradient for outer half of dendrites than do the expt.:

exp ones do all show steep gradient for ~~dendritic trunks~~ prox dendrites than periph.

Now think of primary – secondary smear.
does not seem to explain discrepancies

But how about departure from spherical symmetry?

later firing cells could have their cones act as pathway for earlier firing cells & thus would fail to show zero gradient that would be present in peripheral cones when truly synchronous.

This hypothesis could be checked experimentally by comparing records in anterior & posterior part of cells

Gordon's study of May 31 (1960) does seem to fit this hypothesis

axonal GEC can be estimated by experiments which block mitral cells.

Note that axon (main phase) GEC is caused from ~~MBL to GL~~ GL to MBL

Whereas granule GEC is from MBL to GL

* Records obtained when mitrals block, should provide an approx. to ~~of~~ axon GEC effect, except one must remember that if mitral cells are not invaded, they would not provide dendritic E to granule cells & granule cell GEC would be different. Gordon does have ~~Some~~ some expt'l. results on this & could try for some more. ie. with two per sec, gets block every other time. Needs faster sweep to see well. Should be looked into. See pp 54 & 55

I-b exp. records do not have surface pos. to theoretical ones & this reduces gradient.

Presumably afferent axon GEC accounts for this. i.e. it pulls surface neg by some fraction of the deep neg.

~~Not the case with spit~~

I-C expt'l gradients are nearly flat

passive theoretic dip at MBL

shaped active dips of cpt. 8 } indicative of dendritic firing.

synch active dips of cpt. 5 }

I-II transition (MBL at zero)

even passive cases have neg dip (PL)

prox. dendrites serve as passive sinks for repol. soma & for the less depol. dendritic periphery.

.9044 does not dip.

exp. ones show very slight dip as well as a general gradient from MBL to GL (which must be early granule GEC

II-b+C theoretical show gradient from MBL to GL but very little deeper than MBL

exp. show domination by granule cell GEC gradient.

10/26/64

Dr. Gordon Shepherd
c/o Dr. David Ottoson
Fysiologiska Institutionen II
Karolinska Institutet
Stockholm 60
Sweden

look back at extracellulars for antidromic block

see p. 30

64795.9053 blocked

	gp. 1	2	3	4	5	6
intracellular peak spike	.941	.939	.918	.170	.153	
KT	6	9	12	15 & 16	17	

did not die and properly.

zero gnd cond, peak	-.222	-.286	-.337	-.236	-.153	-.09
KT	14	12	13	15	15	16

p.d. factor = .25	-.177	-.246	-.292	-.189	-.107
KT	13	12	13	15	16

amplitude of peak neg is about 15% of that for unblocked

* Restudy page 29 *

another blocked case is 64795.9032 see page 17

	1	2	3	4	5	6
Intracell peak	.94	.93	.91	.143	.128	.117
KT	6	9	13	16	17	18

decay passively

Zero Shunt Conduct.

neg peak	-.183	-.25	-.302	-.1905	-.123
KT	14	13	14	15	16

This is about 15% of unblocked (see .9031)

and occurs close to time of hillock spike peak

which peaks at KT=18

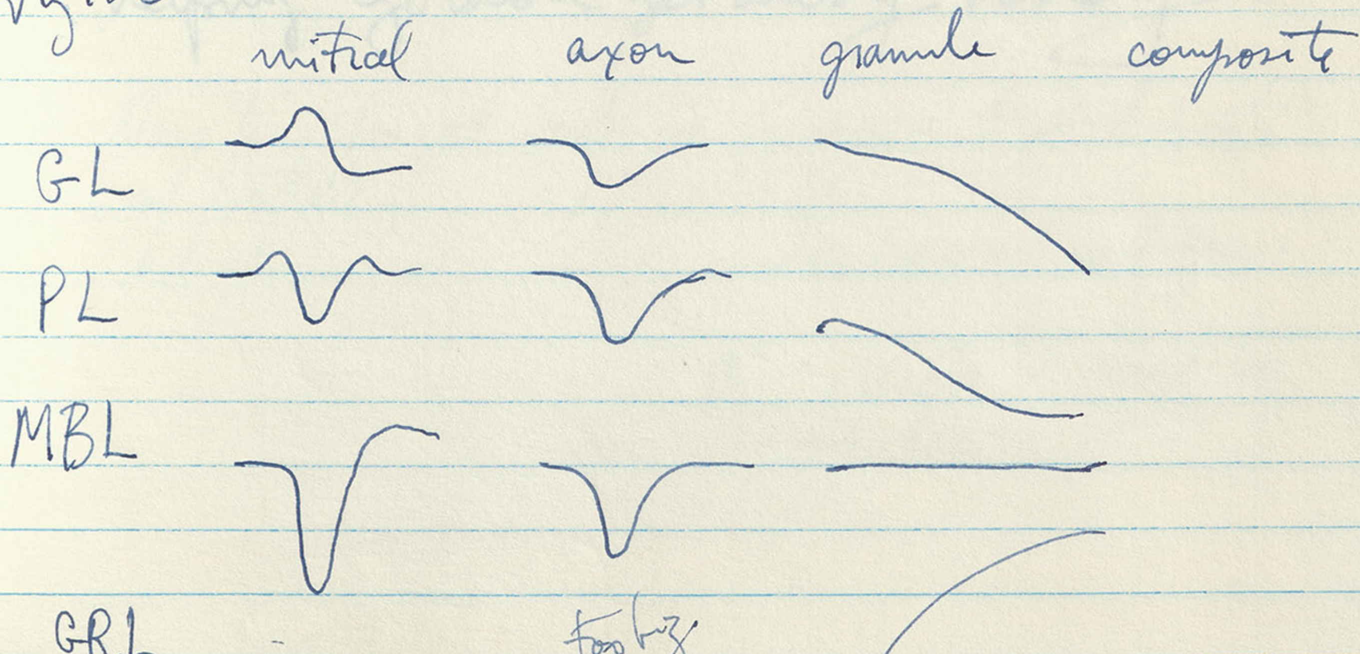
ampl = -1.87

similar result with block in .9023

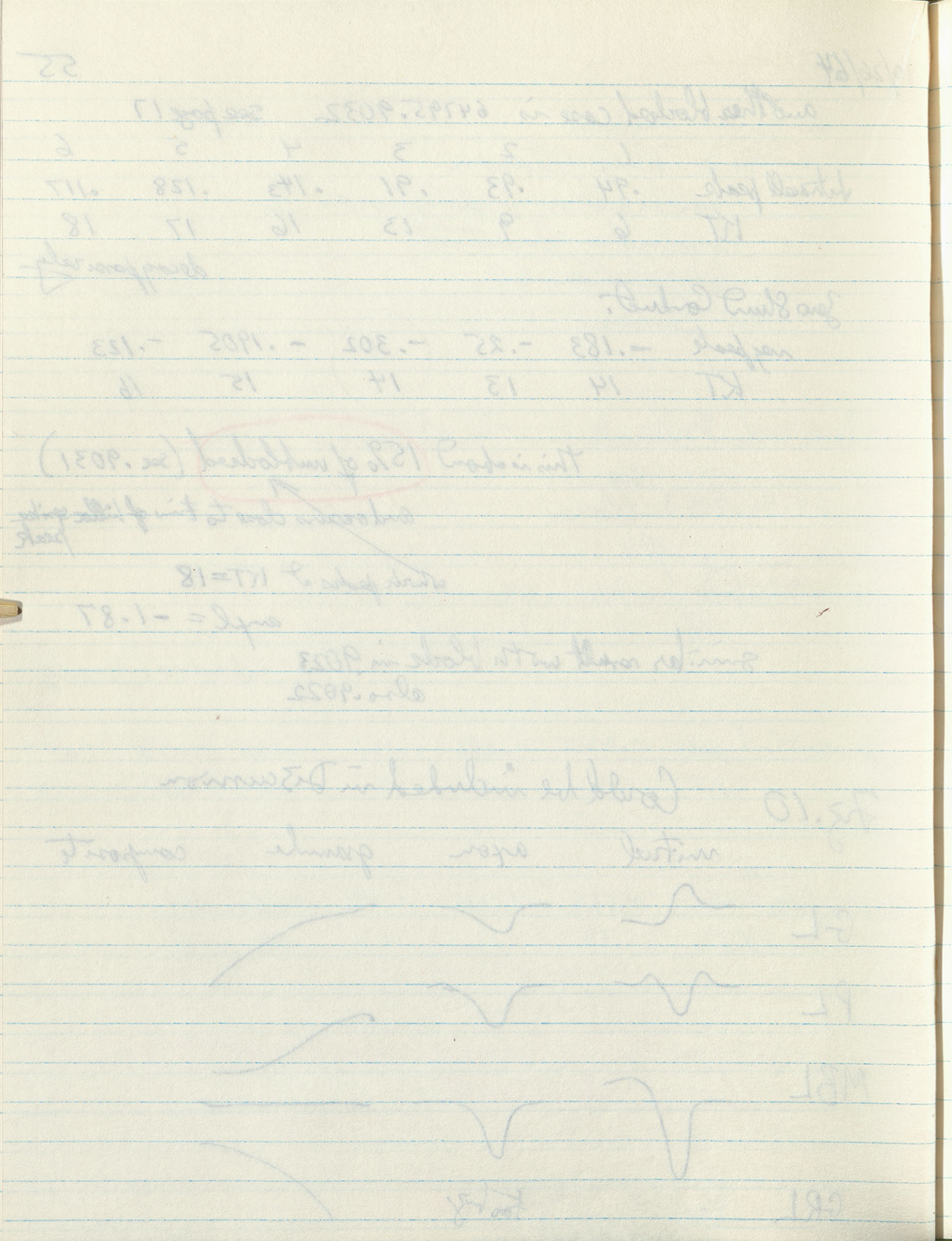
also .9022

Could be included in Discussion

Fig. 10



Foo fig



Since it is probable that paper ~~II~~ will appear significantly later than paper I, perhaps we should say a little about granule and axon superposition with mitral & present one or two tentative reconstructions.

Paper II would go into more detailed discussion & justification & perhaps also other kinds of plotting.

Inspection of Jordon's blocked mitral cell records shows a residual peak that is one third to one half of that with invasion.

Did succesful reconstructions between helping Gordon get away today

10/28/64 – 11/2/64

after Gordon's departure

(1) rearranged bookcases to provide for additional storage

(2) Put all Aitken data analysis away together

(3) Collected information on Federal Employee Health Benefit program for presentation at Assembly Meeting.

(4) Prepared memo on same

(5) Prepared semi-annual report on "Scientific Accomplishment"

(6) Sent reprints to several recent requests.

(7) replied to Fender's Cal. Tech invitation

(8) replied brief note to Stark re Gordon Conference

Now time to get back to figures & 2nd draft of paper.

↓

esp. reconstructions.

also, photo to send to Gordon

Must work out a justification for diffusive axonal contribution

11/4/64

Today completed a final pencil version of superposition Remarkably Successful

A. mitral #4795.9041

+B. axons diphasic graded

+C. granule similar to computed

=D. superposition

for four depths GL, PL, MBL & GRL

Also fixed time dotted baselines of Fig. 2 to be ready for photography.

Also fixed figure 1-B to provide horizontal collateral #6 and short axon #7

as well as level designations GL, PL, MBL

Also "GLOMERULUS" inside the circle

11/5/64

Completed, with black tape & Leroy lettering
took to Photography

I - Fig. 1-B diagram

II - Fig. 2 exp. series

III - Fig. 3 Three records with Periods I, II, III.

Also, took to Medical Arts the pencil figure 10 which shows Superposition (See previous page)

Now, must set up additional calculations with DT = 0.002 if NT sufficient
for 9041, 9044, 9045, 9059

need smaller cpts.

9160 replace with QB = 25?
& with end cpt M_{jj} same as for others

See p. 42

See over

Revise text - see pp 43-48 of this notebook.

Halving dendritic pts doubles ~~Gd~~

~~there~~ i.e. for $\Delta z = 0.1$, get $UD = 100$
for $\Delta z = 0.05$ get $UD = 400$

See pp 61-62 of book 3

Factor of four can be seen as

$$UD = \frac{GD}{CD} = \frac{\text{double}}{\text{half}} = \text{four times}$$

$$USD = \frac{GD}{CS} = \frac{\text{double}}{\text{unchanged}} = \text{double}$$

12/14/64 refer back to book 3 p. 62 ¶ ahead to p. 82 of present book

10 pts.
suppose now $LD = \frac{1}{2} LA$, because $LA = LD$ for 5 pts.
then $\frac{\mu D}{\mu A} \neq \frac{DD}{DA}$

but $\frac{\mu D}{\mu A}$ = four times previous
But I already got this from $(\Delta z)^2$ ~~wrong~~ Considerations

$\frac{\mu SD}{\mu SA} = \frac{GD}{GA}$ = ~~four~~ twice previous

but then this changes λ_{ij}

64795.9141 based on 9041 with more dendritic cpts & smaller DT

1 64795.9141 251 8 .002 .05 0 0 0

2 0

3 25. 400. ~~25.~~ 5. 400. 1. 3 10 0 ~~1001~~ 1111 +1

4 5. .0 .0 .0 .3 .3 .3 .3 - - - - - - - ten of these

~~4~~ 600. 5. 100. 25. 40. 5. 50. .10

6 4. .25 .2 1.3 1.7 .04

Also let 64795.9142 be the same except that
card 3 has iflat = 1001
card 4 has VEF = ~~3.33~~ 4.77
$(4.0)\left(\frac{20}{14}\right)\left(\frac{5}{6}\right)$

64795.9144

1 " 251 8 .002 .05 1 0 0

2 0

3 25. 400. 5. 400. 1.0 3 10 0 1101 -1

4. 5. .0 .0 .1 .1 - - - - - - eleven of these

5. 400. 1. 25. 20. 40. 5. 40. .10

6. 4. .28 .1112 1.3 1.7 .04

~~7111+99~~ .0 .0 .0 .01 - - - flat - - -

7111+99 .0 .0 0 all zero

9143 could be the same with QB = 25.

Expect ≈ 120+180 = 300 secs for 9145
9160

But the other two will be 4X as much in the Runge Kutta – Maybe 600 secs ~~each~~

~~for 9141, 9144, 91~~ roughest time

		pages		Actual time
9141	600	28	1111	411
9144	600	28	1101	
9145	300	23	1101	250
9160	300	28	1111	342
60	1800	102		
	30			

64795.9145

1 " 251 2 .002 .1 0 0 0

2 0

3 as before 25. 100. 2.5 100. 1. 3 10 0 1101 +1

4 .5 .0 .0 .0 .25 - - - flat - - -

5 600. 5. 100. 25. 40. 5. 50. .10

6 4. .25 .1112 1.3 1.7 .04

64795.9160 based on 9059 but with QB=25.

1 " 251 2 .002 .1 1 0 0

2 0

3 25. 100. 2.5 100. 1. 3 10 0 1111 -1

4 5. .0 .0 .1 - - - flat residual fail

5 400. 1. 75. 20. 40. 5. 25. .10

6. 4. .25 .1112 1.3 1.7 .04

+1+1+99 .0 .0 .0 .0 .04 .03 .02 .01 - -

+1+1+99 - all zero

Boards ready 10:30 AM 11/6/64

Now look at program revisions see p. 42

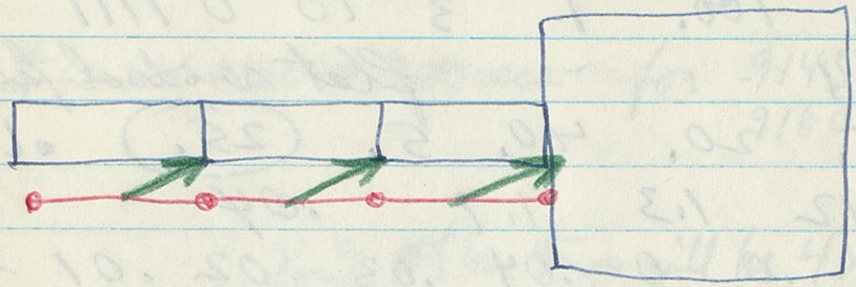
Dave 11/6/64 mod. 451, 452, 455, 462 & program numbers

Also get rid of RINC & RINB in main program (anachronistic)

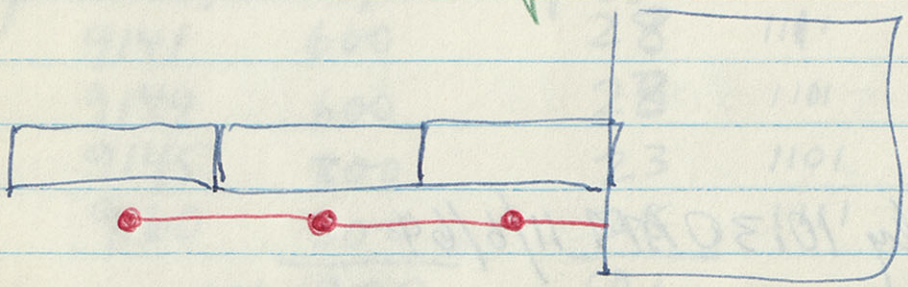
Also, using matching ARGS & put Equivalence statements in Subroutines

This did not work

2/21/67
use FAC = 2. to
and later plan to
fit into wiring format



Red represents core resistance, and when assigned to connections as shown in green, we get what has been used so far.



Just modified WXR795C → WXR796C
93C → 96C
94C → 97C

Cleaned up old RINC+RINB, also QUENCH:QENCHA & GD:UD etc. taken care of by Subrout. args

Most important changes were.

(A) smaller tests at 455 & 462 to prevent fictitious local response in the long period runs.

? * (B) put in factor of (2.) at 451 & 452 to make U_{ij} the same for end compartments as for in between compartments.

Rationale ~~is that~~ was that g would be twice as great at ends, but not so sure now.
Really ought to be treated by the more careful method Jim uses for lumping.

The intuitive argument is fairly clear for doubling g at the axon soma jam, but this was not, in fact, done
Better Ponder & Reconsider this.

11/10/64 got results on 64795. 9145
9141
9160

see p. 61

9144 did not run because of error in cards.

.9145 agrees with 9045
The extra time values will be a help. The gradient plots were probably close enough.

.9141 does not agree exactly with .9041
This shows even in the intracellular volumes of compartment (1). Examine more closely.

UA & USA are 25. and 5. in both cases
UD & USD differ

in 9041 UD = 100. USD = ~~2.00~~ 200. ~~if there~~ NSD = 5
9141 UD = 400. USD = 400. NSD = 10

∴ in 9041, U_{ss} = 206.
in 9141, U_{ss} = 406.
} this is probably not desirable

should leave USD same as before and change only UD

Therefore set up 9241 with USD = 200., UD = 400.
also 9244 " "

Also, set up 64796.1160 to test new program on this question of large and intracellular spike.

This speech will be published in book "Nerve as a Tissue"

Sir John Eccles' dinner speech was rather interesting.

focused on reminiscenses, scientific method, scientific spirit + tremendous scope + future for neurophysiol

a) commented on how fortunate he had been to join the Sherrington school at the peak of the classic neurophysiol. era. No substitute for working with a great scientist.

b) commented that he had uncritically accepted the erroneous inductive concept of scientific method which purported to get results from an accretion of data. That (around 1945) he had been very depressed when he realized that data was disproving the electrical hypothesis for neuromuscular junction, where he had pretty completely committed himself to the electrical hypoth. (i.e. he felt that a cherished belief was being destroyed) Karl Popper saved the day for him by convincing him that science

c) progresses through the falsification of hypotheses. The disproof of a hypothesis should be a cause for rejoicing rather than dispair. This gave him a new lease on life, but, of course, he prefers to be the one who disproves his hypotheses. He was very definite that hypotheses should not be secure, but that they should be definite & clear & provide a clear target to be shot at. He also praised

d) the free level of personal communication amongst neurophysiologists; implied that there was remarkably little petty competitiveness - rather paradoxically prior in view of his own record. Said that friendships continued in spite of sharp scientific disagreements. He also commented that it is better to be challenged in print than to be ignored.

e) he ended on the note one reason for the lack of bitter competitiveness & lack of trying to keep a problem to oneself, is that there is so much to be done. There are enough problems for everyone, the field is wide open. Each success opens up more. The program of understanding the mechanistic aspects of the brain extends at least several generations into the future; into the next century or more. He implied, but did not dwell on the thought that the "brain-mind" problem could be postponed that long. He was, in fact, fuzzy, re brain-mind distinction. see next pg

Just returned from Nerve as a Tissue Conference

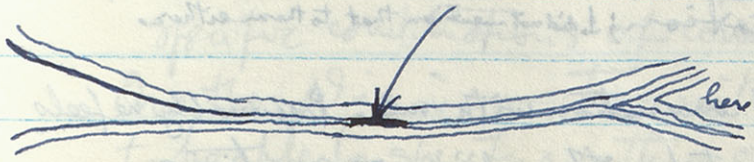
Saxo Sir J. & Mrs. E, Cole, Windle, Schoffle, Curtis, Hubbard, Willis, Vander Loos, Farley, Stanley Crane, Bornstein, Barbara Rankin, Brindley
↳? Goldensohn?

Poley - glia coat dendrites except at synapses
at synapses, glia seem to envelope synaptic pairs & isolate them from synaptic groups on other dendrites.

showed slides with glia blacked in to show how ubiquitously it fills spaces between dendrites & axon terminals.
Yet, he is ready to allow for 5 to 15% extracell space.
Robertson has seen some much more open.
He is doing some expts. to purposely open things osmotically.

Pappas - Bornstein, Cohen, Bennett
They have shown electrotonic synapses in tissue culture of embryo mouse cortex.
They see axo-axonic
soma-somatic
electrotonic
Jens.

Double membranes come together & their hydrophilic layers seem to fuse at so called electrotonic



Standard synapses have granules on presynaptic side. Electrotonic ones don't.

Got through this dinner with Curtis + Hubbard & Willis + Barbara Robbins. Curtis & Hubbard chuckled at many points (the atmosphere was already genial from cocktails & from "old goat" speaker previous). At end of talks, Curtis turned to Hubbard during the clapping & said, "and he does it all on ginger beer".

I could sort of join in the feeling with Hubbard, afterwards, that they were well aware that JGE does not live up to all those pious phrases, but that, nevertheless, they do admire him, and that many of the pious phrases are worth emphasizing even if he doesn't live up to them. In other words, he does pay lip service to & even largely believe in the right sort of values.

However, it was also apparent to me that Curtis & Hubbard survive at Canberra because (1) they are very good, (2) they try to be independent (3) they are able to laugh at the big man's many foibles & they seem to do this all the time.

They mentioned many times how impressed they were with Lloyd for having been the first to reply to the Festschrift invitation & the first to send in his manuscript. With regard to profit from Eccles Spurgeon volume, they commented that he had given 900 copies away.

They were aware that after Eccles had done his hatchet job on Lloyd, he had passed Coombs to dig out the old records relevant to my paper & had carried the same mood over to that. They did not seem to be aware of his attempts to block my publication; I did not mention that to them either.

It was my impression that he evaded conversation with me. Presumably he feels guilty & does not want to be confronted with embarrassing questions.

Set up new production runs.

64795.9241 like 9141 but with USD = 200.

also 64795.9244 "

and add missing card of 9144

set up 64796.1160 on test, need to satisfy CRT limit

Received today, letter from Ramon-Moliner. He regards [redacted] cells as "preamplifiers" of the nervous system & he likes my safety factor argument for making this a redundance device. He does not mention the idea & I wrote to Pat Wall in 1961 regarding protection against noisy endings, but he does say that preamplifiers should be [redacted] low noise. He also calls attention to the granule cells of the olfactory lobe as having only dendrites and wonders how they might function. This makes me wonder if I should not write two short notes to Science, one on this low noise-redundancy idea (with references to personal communications) and one on the granule cell idea.

Also, today, I was thinking about the application of my dendrite models to nerve nets & the fact that one needs to set up specific combinations of connections for specific purposes. One thought is in connection with pattern recognition. One ought to be able to specify a pattern of connections that would recognize circles of certain radius, for example. Thus, [redacted]

down stream from receiving zone, there would be a cell, or a group of cells which would respond only when the excitations & lateral inhibitions were such that they satisfy the constraints for a circle of this diameter, whatever its precise location. Slightly different group of cells for circle of different diameter.
If circle broken, or say, a semicircle, this would be indicated by additional cells.

Try to define this,

Let O_{10} designate a cell responsible to circles of radius ten units.

Digress for a moment, note that dendritic location of endings would permit also the temporal sequence along a curve to be detected. It is possible that the Hubel & Wiesel lines have a directional sequence aspect that has not been looked for.

Assay the primary neurons (or retinal cells) P_{11} P_{12} P_{13} P_{14} ...
P_{21} . . . . . .

Each secondary neuron could, even, disregarding dendrites, have input $SI_k = \sum_{ij} A_{ij} P_{ij}$

Circle secondaries would be those for which A_{ij} of significant mag. could have ij pairs satisfying circular locus in the ij plane. This would be OK as purely formal, but it would be nice to go more detail about how achieved.

Remarkable coincidences

① Ramon Moliner's letter received yesterday raised subject of granule cell which Gordon & I had discussed.

② middle of p. 66, yesterday, postulated temporal sequence. Today, new copy of J. Physiol. has a paper

Barlow, Hill & Levick
J. Physiol 173 377-407 (1964)

"Retinal Ganglion Cells Responding Selectively to direction and speed of image motion in the rabbit." — which deals especially with this point.

Should do a little quantitative checking out.

11/18/64 p. 385 10°/sec

middle p. 385 for on center unit, discharge occurs as spot approaches the center, moving from the "off" part to the "on" zone of the receptive field. as soon as it crosses the center of the field & moves away from center, the discharge abruptly slows or stops.

In off-center units, the sequence is usually the exact reverse.

bottom p. 385 deals with concentric-type units, which are different & bear pondering. summation of E + I accounts for ↑ but not for directionally sensitive. block or white spot

bottom p. 387 - spont. firing neuron can be suppressed with wrong direction.

11/18/64 Talked with Bill Hagins on the telephone. He recommended that I write Horace Barlow who is now at Berkeley. He did not think there had been much careful thought about dendrites. He thought I should be in closer touch with exptal groups

Here I am again confronted by conflicting priorities, interests & obligations in my research. I have just written Ramon-Moliner re tufted dendrites and Horace Barlow + Rosalind & Bill Hogues re spatio-temporal patterns, but my first priority should be to finish the work already 3/4 finished. Also, I have to complete something for the Tokyo Congress. For this Congress, my temptation is to discuss spatio-temporal aspects of synaptic inhibition; attempt to summarize the answers to a variety of questions re additivity, effect on epsp of "conductance" when peripheral, difference between J pulses & J background, etc. Other personal priority is to write up the spike model.

This following list was made while in Philadelphia at Nerve as a fissure conference

1. Basic field paper (Gordon now has a copy of this ditto)
2. Ezra & Jeanne
3. Kinetic spike model
4. geometric factors
5. Mitral Cell with Gordon (I and II)
6. J location — see Book 2 degeneracies
7. Tree Generation
8. Aitken story

9. New odd spatio-temporal story re pattern discrimination
10. Also, elaboration of granule cell story
11. Ramon-Moliner & tufted.

Now look back at p.1 and p.5 of Book 4. for older finite dendritic length stuff.

Also Jose & I have been talking about a study group on control theory and non-linear diff. eqns.

Frankenhaeuser presented a talk on his frog node experiments and computations done as sequel to those he did with Huxley.

Stimulated me to feel I should write at least a brief note on my model. Three justifications for simpler model

(1) Expedite computations where fine points are incidental

(2) We don't actually know the H&H params for mammalian nerve anyway. Why conditions should one choose? Would that be any less arbitrary than my model? Frankenhaeuser would recommend his frog (vertebrate) data, with a temp. correction.

(3) Discovery of any deficiencies, re H&H & expt. would provide added insight on whole problem.

Frankenhaeuser's main reservation was that model should respond correctly to current pulses during spike. He also was concerned that current safety factor might be incorrect.

Obviously, a brief presentation would have to touch upon some of these questions.

Now, must return to Fig. 4 of mitral paper & consideration of cones & spherical symmetry (cf. pp. 45+46 & 34 of this book)

Worked on Mitral Manuscript
Also got off letters to Fender & Gordon Shepherd & began one to Perkel

Notes regarding Perkel's Rand Memo – RM-4132-NIH June 1964
A Digital-Computer Model of Nerve Cell Functioning.

11/30/64

on page 8, Q is quantity of transmitter released
on pp 6 & 7, depletion & restore of reservoir is like Liby & North (early appendix
J. Neurophysiol 16 509-527 (1953)
appendix pp 521-525
(use Q is inhibitory (naive))

p.9 incorrect – Why use Langmuir absorption isotherm.
Trouble here is that he is using the wrong reference potential. p.10 indicates awareness that something is wrong, but not what the cause of the trouble is.

pp 16-17 discuss short comings
p.37
confuses q_i "charge" of i^{th} efferent channel
with q_i "charge" delivered to post synaptic membrane
wants rate of removal to be $q_i \lambda_i e^{-\lambda_i t}$ from efferent channel
& says this is to be equated with rate of augmentation of the cell potential ! Pretty fuzzy
Equations (17) and (18) are incorrect
presumably should be $\frac{dP}{dt} = -\lambda_c P + \sum_i \lambda_i (q_i/c) e^{-\lambda_i t}$
because then $c \int_0^\infty \lambda_i (q_i/c) e^{-\lambda_i t} dt = q_i$

But I would add that for excitation, one should include the factor $\left(\frac{E_E - V_m}{E_E - E_R}\right) = (1 - V_0)$, and for inhibition, one should include the factor $\left(\frac{E_I - V_m}{E_E - E_R}\right) = (\beta - V_0)$

Because, for very brief Δt ΔE, my model gives postsynaptic

~~$Q/C = (E_E - V_m)\Delta E \Delta t$~~

from Ojai eq (1)

~~Δ~~

$$\Delta\{C_m \dot{V}_m - I_m\} = (E_E - V_m)\Delta G_E$$

$$Q = (E_E - V_m)\Delta G_E \Delta t$$

~~$\Delta \dot{V}$~~

$$= (E_E - V_m) G_R \Delta E \Delta t$$

$$Q/C = (E_E - V_m)\left(\frac{1}{\tau}\right)\Delta E \Delta t$$

$$= (E_E - V_m)\Delta E \Delta(t/\tau)$$

Also, if $\frac{q}{C} = \frac{Q}{C(E_E - E_R)}$, then

$$q/C = (1 - V_0)\Delta E \Delta(t/\tau)$$

This can be related to eq. (10) of Ojai paper as follows.

if $\Delta J = 0 = \Delta\chi$, and if $\Delta \dot{v}$ is const for brief Δt

then $q/C = \Delta \dot{v} \Delta t = \Delta v$

$$\hookleftarrow (1 - V_0)\Delta E \frac{\Delta t}{\tau}$$

However, now, to avoid using square pulse or δ pulse of current, me of conductance

try to use the notion that $Q = \int_0^\infty I\,dt = \int_0^\infty \lambda i Q e^{-\lambda i t} = \left[-Q e^{-\lambda i t}\right]_0^\infty = Q$

This is equivalent to flow from a neighboring compartment.

But, having noted this much, should try to become explicit about the shortcuts for dendritic model that I have considered before, but not written down. Following points.

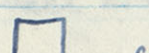
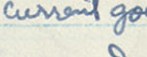
(A) when not at recording site, it may be good enough to have $\delta(t)$ of current which gives instantaneous Q & hence a sharp voltage change, but must have the Q depend upon $(1-V_0)$ or $(\beta-V_0)$

(B) This works OK when $\mathcal{E}$ & J are in same compartment, except that if J stays on, this has to be included in decay const.

(C) In other words, must clearly distinguish brief $\mathcal{E}$ & J from sustained.

(D) Furthermore, even when at site, one could avoid abrupt voltage change by backing off from δ current. ~~One pa~~ Three possibilities (a) constant current for Δt, (b) $\lambda_i q e^{-\lambda_i t}$ as incorrectly implied by Perkel, or (c) exact, ~~###~~ a la conductance i.e. proportional to $(E_\mathcal{E}-V_m)\Delta\mathcal{E}$, (d) approx. to this could be done with linear change in V taken into account i.e. initially have factor $(1-V_0)$ & change linearly to $(1-(V_0+\Delta V))$.

(E) However, if we consider possibility that conductance pulse need not be squarely turned off, then (b) looks better again.

Note, for square conductance pulse  , current goes  ,
but, $\mathcal{E}$ conductance pulse  , current goes 

if $\tau\dot{V}+V = \mathcal{E}(V_\mathcal{E}-V)$ ~~has soln $V \propto e^{-\lambda t}$ for V initially zero~~

what must be the time course of $\mathcal{E}$ such that $\mathcal{E}(V_\mathcal{E}-V) \propto e^{-\lambda_i t}$

Trouble is we have the product of two variables here

$$V_\mathcal{E} L_t\{\mathcal{E}\} - L_t\{\mathcal{E}V\} \propto \frac{A}{s+\lambda_i}$$

$$\therefore V_\mathcal{E}(s+\lambda_i) L_t\{\mathcal{E}\} = (s+\lambda_i) L_t\{\mathcal{E}V\} + A$$

note that $A \propto Q(V_\epsilon - V_0)$ see p. 76

12/1/64

We have

$$\tau \dot{V} + V = \mathcal{E}(V_\epsilon - V) = A e^{-\lambda t}$$

here A has dimension of voltage

for $V(0) = 0$, outer pair give $\overline{V}(s+\tau) = \frac{A}{s+\lambda}$

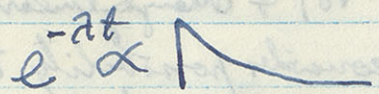
$$\overline{V} = \frac{A}{(s+\lambda)(s+\tau}$$

add $V_0 e^{-t/\tau}$ for nonzero I.C. $\quad \therefore V(t) = \frac{A}{\lambda - 1/\tau}\left(e^{-t/\tau} - e^{-\lambda t}\right)$

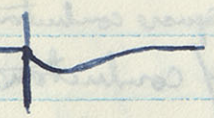
Now, we can solve for $\mathcal{E}$ see p. 76

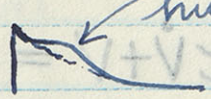
$$\mathcal{E} = \frac{A e^{-\lambda t}}{V_\epsilon - V} = \frac{e^{-\lambda t}}{(V_\epsilon/A) - \left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - 1/\tau}\right) - \frac{V_0}{A} e^{-t/\tau}}$$

$$= \frac{A}{V_\epsilon e^{\lambda t} + \frac{A}{\lambda - \frac{1}{\tau}}\left(1 - e^{(\lambda - \frac{1}{\tau})t}\right)} = \frac{A e^{-\lambda t}(\lambda - \frac{1}{\tau})}{V_\epsilon(\lambda - \frac{1}{\tau}) + A(e^{-t/\tau} - e^{-\lambda t})}$$

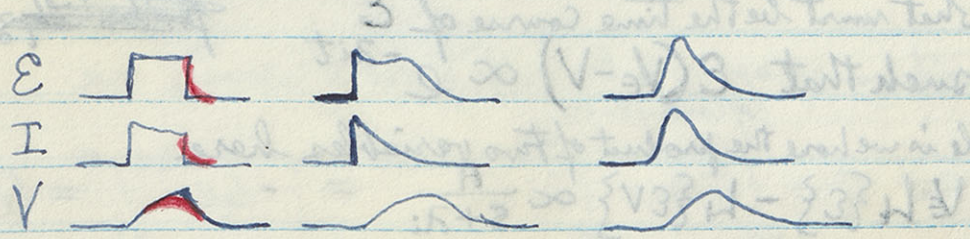
Not hard to plot $e^{-\lambda t} \propto$ 

$V \propto$ 

$V_\epsilon - V \propto$ 

$\mathcal{E} \propto$ 

hump due to λ in denom.



see p. 76

To have $\mathcal{E}(V_\epsilon - V) = Ae^{-\lambda t}$

One can get a solution of the following kind
Don't yet know anything about uniqueness

Suppose $\mathcal{E} = Be^{-\lambda t} + F(t)$

$\mathcal{E}V_\epsilon = BV_\epsilon e^{-\lambda t} + V_\epsilon F(t)$

~~$\mathcal{E}V = \dots e^{-\lambda t}$~~

above can be satisfied if

$$\mathcal{E}V = (-A + BV_\epsilon)e^{-\lambda t} + V_\epsilon F(t)$$

and $$V = \frac{\mathcal{E}V}{\mathcal{E}} = \frac{(BV_\epsilon - A)e^{-\lambda t} + V_\epsilon F(t)}{Be^{-\lambda t} + F(t)}$$

But we know that $V = \frac{\lambda A}{\lambda - 1/\tau}\left(e^{-t/\tau} - e^{-\lambda t}\right)$

so that we could try to solve the above for $F(t)$?

Note from eq(10) of my Ojai paper, for small Δt and with $\Delta j = 0 = \Delta\psi$

get $\Delta v \cong \dot{v}\Delta t = (\dot{v})_{o-}\Delta t + (\Delta\dot{v})_o \Delta t$

$$= -\mu\Delta t(v_{o-} - v_{s_o}) + (1 - v_o)\Delta\mathcal{E}\,\Delta t/\tau$$

↓ this term is zero if $v_o = v_{s_o}$

But otherwise get $-\Delta t\left\{\frac{v_o}{\tau^*} - \frac{\mathcal{E}_o}{\tau}\right\} = (v_{o-} - v_{s_o})\left(\frac{\Delta t}{\tau^*}\right)$

where $\tau^* = \frac{\tau}{1+\tau\mu}$

in other words, this is the rate of previous approach to v_{s_o}

12/1/64

12/2/64

As usual, I am torn between several projects & at the moment, have spinning in my head, titles & opening paragraphs for four different projects, not to mention the Mitral Cell paper.

(1) for Physiol Congress Abstract

"Potency of Synaptic Inhibition"

could be short title, and then go on to say that will discuss factors which determine potency in various soma-dendritic spatio-temporal patterns of synaptic activity.

(2) Ramon-Moliner will be in Town today. Note with him could begin. Title - Significance of Dendritic Tufts of Secondary Apical Neurons. "We begin with the colorful remark that the dendritic tufts help these neurons play a pre-amplifier role. X Introduce preamplifier word as suggestive or provocative, but add that the analogy is not meant to be carried too far.

(3) This interdependence of E, I, V on pp 72 & 73 Could, of course, choose to make E have a gradual onset, but there is not too much point in this. Also, note that this type of I comes from neighboring syts. anyhow; Actually, in general, should let E & I & V be like sums of exponentials with different delays, but then can crudely approx by $I \propto e^{-\lambda t}$ where λ takes care of smear & initial delay is taken care of separately. Question is, how fully can these simplifications be made consistent with whole.

i.e. question of valid short cuts.

(4) Thoughts about action Potential model paper (cover)

Answer given in following paragraphs: but first make two comments. The model to be presented here ~~has many pros~~ belongs to the family of models that has been discussed by FitzHugh.

12/2/64

Possible title:

"A Simpler Mathematical Nerve Action Potential Model"

It seems best to begin this paper by asking and answering the following question: Why bother with alternative mathematical models of nerve action potentials when the Hodgkin-Huxley model has proved so successful? My answer is that a simpler model can have advantages for certain purposes, such as the following: ~~(1) The a simpler model may permit a very great saving in modeling~~ (1) There are many problems related to axon-soma-dendritic geometry and problems related to networks of neurons which are sufficiently complicated ~~that~~ to justify the significant reduction in computation time that can be achieved by a simpler model; (2) Provided that the simpler model is qualitatively and even semi-quantitatively in agreement with the more complicated model, it ~~is to be~~ merits consideration as a tool in the investigation ~~of problems of~~ tissues whose Hodgkin-Huxley parameters have not been determined (because then it is only qual or semi quant also). (3) In the sense of the class of models discussed by FitzHugh, we may gain considerable insight from comparisons of the adequacy of these models in various tests: it provides a way of distinguishing what is most essential from what may be accidental, special, or even misleading.

Actually, in paper, it may be desirable to have a brief paragraph on each of the above; each with appropriate subtitle. See also p. 69 of this notebook

where Tr represents trigger or transmitter quantity or something equivalent and λ is needed to normalize; $\lambda e^{-\lambda t}$

where T_R represents trigger or transmitter quantity or something equivalent
and λ is needed to normalize; $\lambda e^{-\lambda t}$

12/2/64

$$\tau \dot{V} + V = A e^{-\lambda t}$$

$$V = A\left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - 1/\tau}\right)$$

for $V(0) = 0$

and $$\mathcal{E} = \frac{e^{-\lambda t}}{(V_e/A) - \left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - \frac{1}{\tau}}\right)}$$

let $\tau = 5$ msec and $\lambda = \frac{10}{\tau} = 2\ \text{msec}^{-1}$

for $V(0) = 0$
$A = 1 * V_e$

t_{msec}	$e^{-.2t}$	e^{-2t}	$e^{-.2t} - e^{-2t}$	$\frac{e^{-.2t} - e^{-2t}}{1.8}$	$1 - \text{this}$	$\mathcal{E}$
					1.0	1.0
.1	.9802	.8187	.1615	.0898	.91	1.08
.2	.9608	.6703	.2905	.1614	.84	1.145
.3	.9418	.5488	.3930	.218	.782	1.205
.4	.9231	.4493	.4738	.263	.737	
.5	.9048	.3679	.5369	.298	.702	1.29
.6	.8869	.3012	.5857	.325	.675	
.7	.8694	.2466	.6228	.346	.654	
.8	.8521	.2019	.6502	.361	.639	1.33
.9	.8353	.1653	.6700	.372	.628	
1.0	.8187	.1353	.6834	.380	.620	1.32
1.5	.7408	.0498	.6910	.384	.616	1.2
2.0	.6703	.0183	.6520	.362	.638	1.05
2.5	.6065	.0067	.5998			
3.0	.5488	.0025	.5463			
4.0	.4493	.0003	.4490	.25	.75	.60
5.0	.3679					
	.1		.1	.055	.945	.105

12/2/64 Today Jose had visitor, Dr. Joel Brenner, mathematician now at Stanford Research. He is translator of Gantmacher + other important Russian books + very widely able mathematician.

I presented something on membrane models and also the degeneracies in the middle of Book 2. May 1963 —

See exp. 6/25/63 731,300 series

Summary 7/10/63

Dr. Brenner said that there is a paper by COLLAR in Q. J. Math. (62 or 63) prob can be located in Math. Reviews with title "On Cross-Symmetric Matrices", which may bear upon these degeneracies.

He thought this was worth writing up to bring out the various points.

To complete page 73, note that $A \propto (V_\epsilon - V_0)$ and that, in general, $V_0 \neq 0$

Then $V = V_0 e^{-t/\tau} + A\left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - 1/\tau}\right)$

and $\mathcal{E} = \frac{e^{-\lambda t}}{\left(\frac{V_\epsilon - V_0 e^{-t/\tau}}{A}\right) + \left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - 1/\tau}\right)}$

And if we set $A = B * \left(\frac{V_\epsilon - V_0}{V_\epsilon}\right)$, we get the result

$$\mathcal{E} = \frac{e^{-\lambda t}}{\frac{V_\epsilon}{B}\left(\frac{V_\epsilon - V_0 e^{-t/\tau}}{V_\epsilon - V_0}\right) + \left(\frac{e^{-t/\tau} - e^{-\lambda t}}{\lambda - t/\tau}\right)}$$

Where $B \propto \lambda\tau$ and has dimensions of voltage (see opposite page)

12/3/64

Resolved on Explicit Strategy for getting papers written & reducing the nagging backlog.

* Devote every A.M. completely to writing. Avoid all distractions, such as mail, telephone, conversation and defer these to the afternoon. Stay home if necessary to establish this routine. This A.M. regime should be devoted to one paper at a time. ~~Concurrent~~ Recall the advice of Terrell Hill. Note also that Dick Podolsky told me the other day that he had asked A.V. Hill whether writing had become any easier for him over the years. The answer was no, he still has to go through 7 or 8 drafts; his only advantage over a neophyte is that he knows it will be hard work from the outset & presumably thus avoids some of the confusion & discouragement of the neophyte.

Just for the hell of it, could call this new resolve, project backlog ≡ GOLKCAB, and try to tick off the papers as they are produced. If bright ideas come for other papers etc., as distractions, defer them to the afternoon, but reserve the AM for the particular paper in process.

As of now. Should work first on Mitral paper (also computations figures can be left to afternoons, or deferred, but text must be pressed forward). Then perhaps impulse model next paper, and then potential paper next. based on what I already have.

My usual procedures are fine for advancing several investigations, but not so good for writing.

Now on ditto

Title page

p.1.1 The experimental situation. recording

p.1.2&3 fine print re Fig. 1-B collaterals etc.

* maybe pull last sentence of p1.3 out of fine print.

p.2.1 The experimental records.

p.3.1 Response characteristics at three depths in two periods.

p.4.1 Spherical symmetry and synchrony

p.4.1.1 – exp. facts re. symmetry & synchrony to insert. (but perhaps deferred until later)

p.4.2 details on cone Ω etc., then

Flow of current confined within cones.

p.4.3 Spherical equipotential contours and radial current (perhaps should read isopotential surfaces)

p.4.4 gives equations (1) & (2)

p.4.5 Puncture of spherical symmetry: external current path.

Part I → The Neurophysiological Records to be Analysed

Presentation of ~~The Neurophysiological Problem~~ → ~~Description of Data~~ to be Analysed

Part II Theoretical Significance of Punctured Geometric Symmetry.

12/4/64

Yesterday completed several pages of mitral paper & also prepared ink drawing of Fig. 4-A; may wish to improve arrows for current & new photograph & modify for puncture. Also put dashed lines into Fig. 3. Where do we stand now?

Completed up through cones, but not puncture and external current. The last page of ditto might as well be retyped to modify and cleanup. Perhaps overall heading of this ~~Division~~ ~~Section~~ should be

~~GEOMETRIC~~

(Theoretical Sec.) CONSEQUENCES OF GEOMETRIC SYMMETRY

Theoretical ~~Significance~~ of Symmetry and Puncture.

to separate from earlier expt. sections.

Next section perhaps entitled Punctured Sphere: Extend Path

done today

Next ~~section~~ section: Potential divider effect. (wrote 12/7/64)

Question: Should middle of p. 4.3 to middle p. 4.5 be deferred to an appendix to be treated with resistances?

12/2/64 Wrote up potential disorder effect; perhaps also ~~Shunt Current Effect~~

Telephone call – Creutzfeldt is in town. He & Dieter Lux are to see me this afternoon

Looking at Gordon's draft, I have now replaced all of his section 4, except the part which (a) refers to cylinder inside cone, which may better go into figure legend. (b) instead of Time which I have already deleted twice, and which should come at end of this section, now, altogether. (4.4) has been improved upon.

It may prove possible to present (b) together with Fig. 4c and Fig. 5.

Possibly here, ready for new Division, i.e.

Part III – Response ~~Contribution by~~ Reduced for Mitral ~~Soma~~ Bodies and Dendrites.

⁂ Talked with Creutzfeldt, Lux & Klee.
They study Cat cortex & are correlating intracellular records with surface leads during EEG spindles & strychnine convulsions.

Seems to be a good correlation between intracellular (somatic) epsp & spikes & surface positivity. Fitting idea of extracell. current from dendrites to soma. They were puzzled by sharp surface (+, −) when intracellular spiking was severe, & was able to point out that after pos. probably causes this. This apparently was a new idea to them. Note: They are not dealing with unitary epsp but with bursts epsp & bursts of spikes, hence after pos. is multiple.

12/8/64 Mitral Paper - start to write part III, or last ¼ of part II

Introduction

Part I - Electrophysiological Records to be Integrated Analyzed

Part II - Theoretical Significance of Punctured Symmetry

Part III - Response ~~Deduced~~ Computed for Mitral Bodies and Dendrites (Figs 5 & 6)

Part IV - Latencies and Gradients ~~Deduced~~ Computed for Mitral Model Figs 7 & 8

maybe split Part IV Latencies with Distance
Part V Radial Gradients of Potential

Part V - Discussion & Reconstruction

as transition from II to III, may need to point out what is hypothesis! Also, may need outline of computation

Picked up photography today - Gordon's expt. series
Also Superposition figure
Left to be done - redo Fig. 3 with dashed lines
planar radial Symmetry diagram

12/8/64

Think about Cal. Tech lectures for Mon. 8 + 9, as just confirmed by Fowler. He requests titles, abstracts & reprints or class notes.

Simplest to do as implied by correspondence

I overview of dendritic studies

II details

Did not finish — Appointment with Dentist.

18

for TK = 0.01

	JZ=1	2	3	4	5	
.9041	.4772	.0963	.0400	.2036	.2324	.2884 (7)
.9141	.5272	.1018	.0446	.2134	.2232	.2841 (9)
.9241	.5083	.0987	.0334	.1554	.1816	.2800 (9)

for TK = 0.05

.9041	peak .9431	.5861	.3082	.3003	.2754	.2658 (7)
.9141	past peak .9343	.6438	.3309	.2975	.2840	.2664 (9)
.9241	past peak .9372	.6031	.2889	.2559	.2460	.2452 (9)

low low low

In second two cases, spike in pt. 1 develops a little faster to a slightly smaller peak

.9041 spike in (4) is at KT=16 TK=.15 ampl = .8115

.9141 83 .164 later .7938 smaller

.9142 72 .142 earlier .8918 larger

∴ in 9141, dendrites are definitely more shunt worthy

in 9241, having USD = 200 + UD = 400 makes as though dendritic capacity is reduced as though N halved. set to soma.

See over

12/14/64

The writing regime broke down last week, partly because of insufficient sleep Mon. night & because of dental marathon on Wednesday. Did not succeed in completing pages (after two last Monday) but did succeed in roughing out next part & thinking about outline. To work, the regime may need to have one week rigidly on routine, followed by a week less rigid ~~gestation~~ & then back again, but in any case, mornings largely devoted to writing or matters very closely related to writing.

12/14/64 Afternoon — plan recheck of WXR796C which had trouble when first checked (11/17/64)

Something did not work between main prog & subroutines, conceivably due to new args etc.

First, recheck the programs of (11/9/64) for obvious error

Not obvious

∴ set up with 64796.1201 NT=6, NSTEP=2

IFTEST=81

60 IFAB=0

Also, refer back to pp. 63 + 65

64795-9241 +9244 did not work out as expected.

Must now carefully compare 9041, 9141, 9241

9045	10 dendrites originally	UA 25	UD 100	USA 2.5	USD 100
9041	5 dendrites gpts	25	100	5	200
9141	10 " "	25	400	5	400
9241	10 " "	25	400	5	200

Assuming Rm the same for a axon, soma, dendrites

$$\frac{USD}{USA} = N \frac{GD}{GA} = N \left(\frac{DD}{DA}\right)^2 \left(\frac{LA}{LD}\right)$$

(GD per dendrite)

to change USD without any other changes, corresponds to a change in N. (e.g. 9241)

$LD = LA = 0.04\ mm$
$= 40\mu$

$LD = LA = 0.08\ mm$
$= 80\mu$

$\frac{USA}{UA}$ changed from $\frac{1}{10}$ to $\frac{1}{5}$

$\frac{USD}{UD}$ - - 1 to 2

12/15/64

Take a fresh look at .9041 + .9142

Conclusion is that discrepancy is probably attributable to the difference in fineness of lumping.

First compare 9045 and 9041

In 9045 have NJD = 10 with $\Delta Z_D = 0.1$, ie. UD = 100

$\Delta Z_A = 0.2$, ie UA = 25

Now, we want the total dendritic length to be ZL = 0.5 instead of ZL = 1.0

Suppose we quadruple all R_m (axonal, somatic, dendritic) to achieve this, leaving all diameters unchanged.

note that UA & UD corresp to $\mu\tau \propto (\Delta Z)^{-2} \propto R_m \frac{d}{L^2}$

Clearly, if all diameters and lengths unchanged, then all $\mu\tau$ must be quadrupled.

	UA	UD	USA	USD	UD/UA	USD/USA
9045	25	100	2.5	100	4	40
hypoth.	100	400	10	400	4	40

← But now, if we double all lengths, so that there are only 5 dendritic cpts, then UA & UD are reduced (by a factor of four (because of $\frac{1}{12}$ above, or alternatively because both core G doubled and membrane C halved), whereas USA and USD are only halved, because capacity of soma remains unchanged. This gives (9041)

25	100	5	200	4	40

Vicory

Setup rerun of 9041 with DT = 0.002
and 9341 with USA = 5.5

12/15/64

One could decide to leave LA at 80μ but halve LD back down to 40μ increasing NJD from 5 to 10

This takes us from 9041 to 9141

UA	UD	USA	USD	UD/UA	USD/USA
25	400	5	400	16	80

which should be OK, except for lumping discrepancy.

Alternatively, suppose we changed only Rm of soma and dendrites, but not axon.

Then starting from 9045, would get

UA	UD	USA	USD
25	400	10	400

where LA and LD would still be 40μ & NJD=10

And now, if we double LA to 80μ, but leave LD unchanged, we halve USA and quarter UA

UA	UD	USA	USD
6.25	400	5	400

which differs from 9141 only by factor of 4 in UA

But this is not what is sought either

---

to improve 9141, could fiddle UA or USA or both to try to make soma spike a little earlier and larger. Could try just USA = 5.5 or 6.

12/15/64

setup 64795.9410
9411

where 9410 is same as 9041 except that IFVE = 0
and that DT = 0.002
NT = 115

~~this is to~~ NSTEP = 5 ~~NSTEP~~ 2.5 per .001
whereas 9041 was 1 per .001

∴ this ~~will~~ check adequacy of
step size in 9041 and provide
more detailed DT to compare
with 9141 and 9411
old new

9411 is similar to 9141 except that USA = 5.1
as a fudge to try to improve
over 9141 to fit 9041

Also putting in 64796.1201 see p. 82
as more detailed test of WXR796C

failed & then phoned Moura Hammond & learned
that EQUIVALENCE must not be used for
dummy variables of subroutine argument. Thus
we must delete EQUIVALENCE and restore carefully
matched but non-identical arguments.

12/17/64 Paused to reflect. Also, read symposium on Science & Public Policy (Fed Proc. 23 (#6 Part I) 1964 1267–1284

Handler, Weinberg, Fountain, Finer

Mutual dependence of Research, Univ. & Govt. is a fact & problem is how policies & conditions be appraised for future. Report to Natl. Acad. "to enunciate the principles and philosophy which can serve as a basic policy in the future conduct and administration of federal programs in support of fundamental research" The committee COSPUP chose to restrict consideration to support of fundamental research in Universities.

Concluded that grant program should remain backbone of support. Criterion must continue to be scientific merit. (for basic research) Essential to use scientific panels for this. Avoid problems to diversion from old research to new research by drafting proposals more carefully and more broadly. Other types of support can be used to support weak units or bolster certain geographic areas, or improve scientists

---

Responsibilities of Scientists for success of grants program

(1) conscientious effort to achieve stated purpose of grant (no other right to the funds)

(2) serve conscientiously & willingly on study sections

(3) obligation to Univ. Community to help with teaching as well as research

12/17/64 .9410 agrees perfectly with .9041

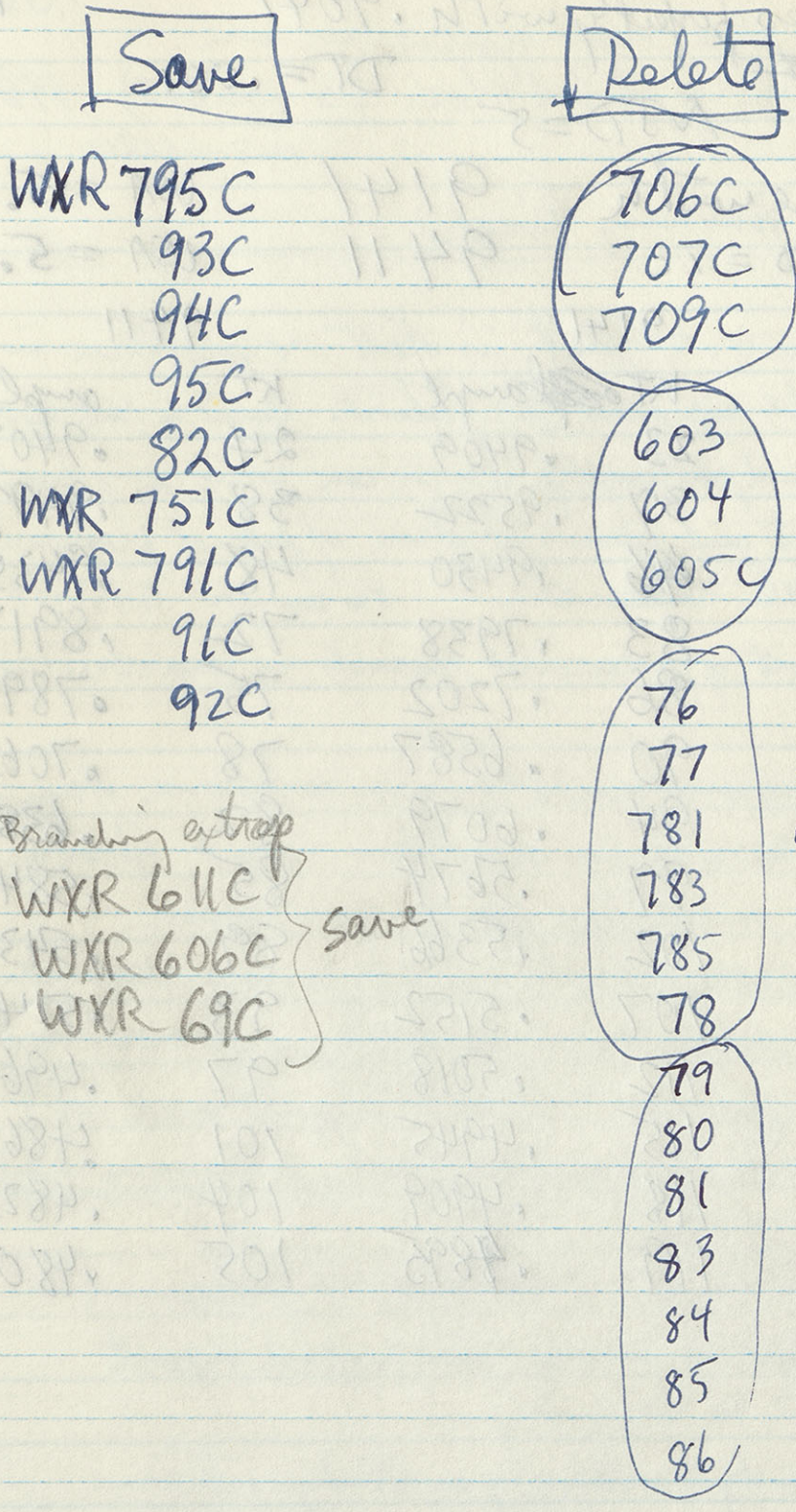
DT=.01 ~~60 usec~~ DT=.001

NJD=5

Now can compare with 9141 USA=15.

both have NJD=10 9411 USA=5.1

Peaks Cpt.		9410 KT	9410 ampl	9141 KT	9141 ampl	9411 KT	9411 ampl
1		25	.9447	23	.9409	24	.9407
2		38	.9526	37	.9522	38	.9497
3		47	.9449	46	.9430	48	.9435
4		77	.8128	83	.7938	72	.8917
5	(5)	84	.6653	86	.7202	75	.7897
6				90	.6587	78	.7065
7	(6)	91	.5645	94	.6079	82	.6387
8				97	.5674	85	.5849
9	(7)	100	.5032	102	.5366	89	.5437
10				107	.5152	93	.5146
11	(8)	108,9	.4757	112	.5018	97	.4964
12				115	.4945	101	.4867
13	(9)	111 ?+	.4674	118	.4909	104	.4823
14				119	.4895	105	.4809


Save
Delete
WXR 795C
93C
94C
95C
82C
WXR 751C
WXR 791C
91C
92C
Branching extrap
WXR 611C
WXR 606C
WXR 69C
Save
706C
707C
709C
delete
12/22/64
603
604
605C
delete
12/22/64
76
77
781
783
785
78
delete
12/22/64
79
80
81
83
84
85
86

12/21/64

Call from Brunelle to delete superseded programs and subroutines from his ~~BRT~~.

Currently using WXR 795C Developed for mitral cell problem. master for axon-soma-dendrite
with WXR 93C, 94C, 95C and 82C
Runge Kutta Ve plot

Not successful WXR 796C with 96C & 97C, 95 & 82 because of Equivalence of dummy arguments.

8/5/63

The compartmental series began with WXR 701C, 71, 72, 73
703 & 706
707 & 709 straight chain
(See Book 3)
780, 781, 783, 785, 786 ~~Soma-dend~~ axon-soma-dendrite

WXR 791C worked well & produced granddaddy series
91C, 92C, 82C

WXR 793C with 93 & 94C introduced 4th power
see pp 15-29 of Book 4

WXR 611C treated subpopulations of Aitken's neurons,
pp 19 and 24 of Book 4
Previous one is 606

WXR 757C kinetics of my spike system.

88

12/23/64 Heavy head cold today. Mild ~~toothache~~ & fatigue yesterday. Presumably much of depressed state of past few weeks has been related to low level toothache and virus. It has happened to me before in December. Obviously cannot rise to any heights of creative writing, but might be able to go over the computer programs that were on BRT that Brunelle called about.

12/24/64 Also talked with Kandel & with Phil Nelson about their anomalous rectification & the effect of R_m or G_j change upon rate of rise of epsp. Wrote letter to Kandel.

12/28 Talked with Phil also about comparing notes with Van Buren on the matter of + and neg amplitudes re ~~&~~ additivity of units.

12/31/64 Got 1/1 reply to Satchel & also some reprints. Toothache now under control with aspirin & Darvon, but this undoubtedly was a major factor in reducing productivity of past few weeks.

Also received & read Gordon's histological manuscript & passed this on to Wade Marshall 12/29/64, to review & discuss with Grant Rasmussen & Paul MacLean

STANDARD FORM NO. 1012a
7 GAO 5300
1012-206

TRAVEL VOUCHER
MEMORANDUM

DEPARTMENT, BUREAU, OR ESTABLISHMENT
DEPARTMENT OF HEALTH, EDUCATION, AND WELFARE, PHS

VOUCHER NO.

PAYEE'S NAME
Wilfrid Rall

PAID BY

MAILING ADDRESS
National Institutes of Health
Building 31 Room 9A-30
Bethesda, Maryland 20014

OFFICIAL DUTY STATION
Bethesda, Maryland

RESIDENCE

FOR TRAVEL AND OTHER EXPENSES
FROM (DATE) 11/11/64
TO (DATE) 11/13/64

APPLICABLE TRAVEL AUTHORIZATION(S)
NO. PHS-3.75483
PHS-3.75483.1
DATE 10/30/64
11/9/64

TRAVEL ADVANCE -0-
Outstanding $
Amount to be applied
Balance to remain outstanding $

CHECK NO.

TRANSPORTATION REQUESTS ISSUED

TRANSPORTATION REQUEST NUMBER	AGENT'S VALUATION OF TICKET	INITIALS OF CARRIER ISSUING TICKET	MODE, CLASS OF SERVICE, AND ACCOMMODATIONS *	DATE ISSUED	POINTS OF TRAVEL FROM–	POINTS OF TRAVEL TO–
A5,154,977	$12.78	PRR	Coach	10/30	Washington, D. C. and	Philadelphia, Pa. return

Physicist

	Dollars	Cts
AMOUNT CLAIMED →	$65	00
DIFFERENCES:		
Total verified correct for charge to appropriation(s)		
Applied to travel advance (appropriation symbol)		
NET TO TRAVELER →	65	00

APPROVED *(Supervisory and other approvals when required)*

F. L. Mills, Assistant Executive Officer, NIAMD

NEXT PREVIOUS VOUCHER PAID UNDER SAME TRAVEL AUTHORITY
VOUCHER NO. | D.O. SYMBOL | DATE (MONTH-YEAR)

ACCOUNTING CLASSIFICATION *(Appropriation symbol must be shown; other classification optional)*
384-34001-84 (2120)

* Abbreviations for Pullman accommodations: MR, master room; DR, drawing room; CP, compartment; BR, bedroom; DSR, duplex single room; RM, roomette; DRM, duplex roomette; SOS, single occupancy section; LB, lower berth; UB, upper berth; LB-UB, lower and upper berth; S, seat.

SCHEDULE OF EXPENSES AND AMOUNTS CLAIMED

PREVIOUS TEMPORARY DUTY *(Complete these blocks only if in travel status immediately prior to period covered by this voucher and if administratively required)*

DEPARTURE FROM OFFICIAL STATION (DATE)	(HOUR)	TEMPORARY DUTY STATION LAST DAY OF PRECEDING VOUCHER PERIOD (LOCATION)	(DATE OF ARRIVAL)

DATE 1964	NATURE OF EXPENSE	AUTHORIZED MILEAGE RATE ____¢ SPEEDOMETER READINGS	NO. OF MILES	AMOUNT CLAIMED MILEAGE	SUBSISTENCE	OTHER
11/11	Taxi to union station					5 00
	~~Lv. Washington, D. C. via PRR 4:00 p.m.~~					
	Ar. Philadelphia, Pa. 6:06 p.m.					
	~~On duty time of arrival until departure~~					
	Taxi to hotel					2 50
	~~Registration fee (No meals or lodgings~~ furnished) receipt attached.					10 00
						~~2 50~~
11/13	~~Taxi to station~~					
	Lv. Philadelphia, Pa. via PRR 4:39 p.m.					
	~~Ar. Washington, D. C. 6:50 p.m.~~					
	Taxi to residence					5 00
	Per Diem: 21/2 days @ $15.00				40 00	
	Grand total to face of voucher (Subtotals, to be carried forward if necessary) →	$65.00			40 00	25 00

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10/26/64

Question: since it is probable that paper II will appear significantly later than paper I, perhaps we should say a little about granule & axon & present one tentative reconstruction.

Why not?

page 1 v 2 last line ? deeper

Consider also Fig. 1-B

or pic 4 on other side

Blocked mitral gives extracell peak ≈ 0.30

The purpose of this brief note is to draw attention to the possible mutual significance of two ~~[illegible]~~ different ~~[illegible]~~ lines of recent neurophysiological research. One is the theoretical study of spatio-temporal patterns of synaptic excitation and inhibition delivered to dendritic trees (Rall, 1964). The other is the experimental demonstration of spatio-temporal ~~pattern~~ selectivity in the responses of ganglion cells in rabbit retina (Barlow, Hill, Levick, 1964).

Case	9045	9041	9141	9241	?
NJD	10	5	10	10	10
ΔL_D	40μ	80μ	40μ	40μ	40μ
ΔL_A	40μ	80μ	80μ	80μ	40μ
UA	25	25	25	25	25
UD	100	100	400	400	400
USA	2.5	5	5	5	2.5
USD	100	200	400	200	200
ΔZ_D	.1	.1	.05	.05	.05
ZL_D	1.0	0.5	0.5	0.5	.5
ΔZ_A	.2	.2	.2	.2	.2
ZL_A	.6	.6	.6	.6	.6
assuming GD = GSD $\frac{CD}{CS} = \frac{USD}{UD}$	1	2	1	$\frac{1}{2}$	$\frac{1}{2}$
$\frac{GD}{GA} \simeq \frac{GSD}{GSA} = \frac{USD}{USA}$	40	40	80	40	80
assuming GA = GSA $\frac{CA}{CS} = \frac{USA}{UA} =$	$\frac{1}{10}$	$\frac{1}{5}$	$\frac{1}{5}$	$\frac{1}{5}$	$\frac{1}{10}$

Introduction

Part I – Electrophysiological Records to ~~be~~ Analysed

Part II – Theoretical Significance of Punctured Symmetry

Part III – Response Computed Deduced for Mitral Bodies & Dendrites

Figs 5 & 6

Part IV – Latencies and Gradients of ~~Mitral~~ Deduced for Mitral Model

Figs. 7 & 8

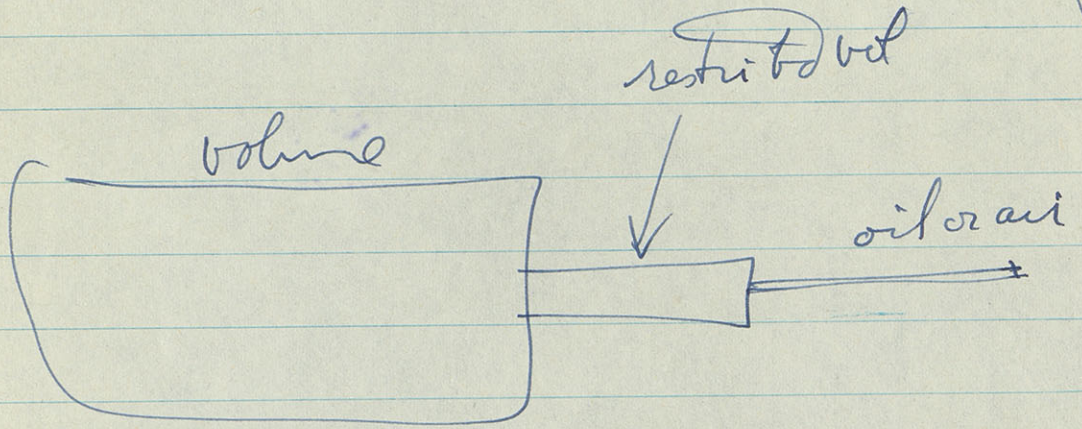
Part V – Discussion

see p. 86 of Book 4

question of dysplasic axon of cortico-tectum?

remember also my thesis input monitor.

This could be checked with a nerve trunk exp.



may have to try with trunk

Write a review for Exp. Neurol.

Calao, Could use some of this in Cal. Tech intro.

In this paper, I wish to ~~place~~ review the revolution that has been taking place in neurophysiological thinking about dendrites. My own ~~study of dendritic~~ ~~properties~~ investigations began in 1956 ~~with a consideration of~~ their cable like properties. ~~These early studies~~ led to

At this time, there was a rather authoritative neurophysiological dogma (which, even, in 1964, seems already hard to believe)

Introduction:

(A short introduction will be added to the final draft. Here is a tentative stab at this.)

Neurophysiologist.

~~A~~ An important objective of much neurophysiological research is to understand ~~the relation between~~ how ~~transients of electric potential~~ the experimentally recorded transients of electric potential

This rese

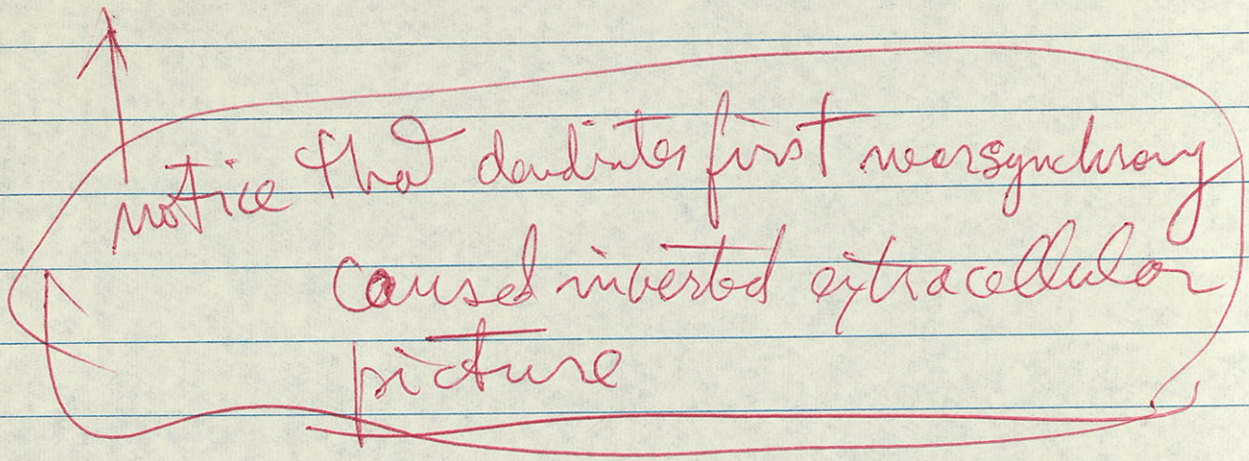
This paper presents the results of an effort at a theoretical reconstruction of ~~the~~ experimentally recorded potentials, as a function of time and of depth in the olfactory bulb.

See semi-annual report.

What is the relation

When the response of a population of neurons is recorded experimentally recorded ~~or the transient~~ → under experimentally reproducible conditions, it is

9064 error in BEB



Possibly serum this erroneous
lose without antidromic & with
loss sonda fail to reduce
synchrony.

VEF = 40

Program could treat end pt. differently (halve C so that UDT terminal = 2.*UD)

9041, 9061 series needs to be redone
with SHCF = 0.
to compare with SHCF = 0.5
& 0.2

3.1

this deals with old fig. 3 which is now postponed.

Fig. 3

A more quantitative description of the direction and magnitude of extracellular current flow during mitral invasion is afforded by the graphs in Fig. 3. Here the potentials at different depths in the bulb are plotted for certain instants of time. The graph in the left covers three instants of time during Period I of Fig. 2; the graph on the left covers the time from the end of Period I through Period II.

The earliest instant of significant non-uniformity in the mitral membrane potential due to the invading antidromic impulse occurs at 1.2 msec, when the extracellular potential begins to move negative at the mitral somata (C in Fig 2) and positive at the dendritic termini (A in Fig. 2). This potential difference is heightened at 1.6 msec, with a correspondingly steep gradient of potential all along the dendritic shafts (slight irregularities can be neglected, as due to unitary responses superimposed on the wave responses). A similarly steep gradient occurs at 2.0 msec, when the negativity at the somata is near its peak, and even the dendritic periphery is at a negative extracellular potential.

shock artefact contribution

A conventional interpretation of these events is that these times cover the progressive invasion of the antidromic impulse into the mitral cell bodies, which are increasingly sinks for extracellular current flow. The dendrites are corresponding sources for these sinks, being at more positive (or less negative) extracellular potentials. Note that the dendrites are sources even at negative potentials; the polarity of an extracellular potential

has no necessary relation to whether it is a source or a sink of extracellular current flow. We will show below that the positive polarity of the dendritic periphery can be merely an artifact of the recording set-up.

We thus conclude that at every point along the dendritic shafts from 1.2 to 2.0 msec., cufrent is flowing outward through the dendritic membrane, depolarizing it. Whether this depolarization is purely passive, or whether it includes a regenerative response of the dendritic membrane, is the question which the mathematical model will attempt to answer.

how about synaptic dendritic spike

no, this applies really to period II

The transition between Period I and Period II occurs at about 2.2 msec. as shown in the right-hand graph of Fig. 3. At this instant the dendritic periphery is continuing to depolarize while the mitral somata are beginning to repolarize. There is consequently no consistent potential gradient along the mitral cell, and hence little extracellular current flow. At 2.6 msec. the potential gradient is just opposite to that at 1.6 msec., because the repolarizing somata are now more positive, and hence current for sources, the still depolarized dendritic periphery. As the activity of the mitral g.e.c. dies away, the potential nonuniformity along the dendrites disappears. The extracellular potentials fall toward baseline, and at the end of the period, at 3.6 msec, the potential curve would be at baseline, with no extracellular current flow, except that now a new potential gradient is beginning because of the action of the granule g.e.c. (Rall and Shepherd, 1965).

Reasons ? 9041 & 9044
to have smaller dendritic
steps.

Passive

5 dendritic
terminal peak ≈ 0.45

10 dendritic
terminal peak ≈ 0.25

↑ flat facilitation as good or better than shaped except for shape of rise of soma spike

eg. 9031 inferior to 9041

facil E should be avoided at soma eff.

importance of control without antidromic

NJD = 5
Period II should be better
(hardplot .9043)

NJD = 10
Period II appears very slow
(Corresp. - Soma spike back to zero with terminals atten. peaks

Ve initial artefact is least when I.C. are flat and soma & peripheral Vi remain close together

Active

(5 or 10 dendritic spts)

flat facil — shaped facilitation (most at soma)

↓ ↓

synch. dendritic spike → $V_e \propto \frac{dV_i}{dt}$ small amplitude

propagated dendritic spike → V_e resembles differencing (nearly equal + & −) larger amplitudes

? minimum at intermediate depths